ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

ERRATA

Page 31, line 2—1939 should read 1839; line 3—1848 should read 1844.

Page 48, following line 18—Insert

Piper aequale var. *laurifolium* C.DC. in Candollea 1:233. 1923, name only.

Page 106, line 19—Syst Veg. 4. Cur. Post. 21 should read: Syst. Veg. 4. Cur. Post. 20.

Page 108, line 24—1788 should read 1790.

Page 110, line 14—*P Williamsii* should read *P. flavispica.*

Page 116, line 7 of key—P. WILLIAMSII should read P. FLAVISPICA.

Page 118, Species 69 should read as follows:

69. PEPEROMIA FLAVISPICA Trel. in Contr. U. S. Nat. Herb. 26:48. 1927.
Peperomia Williamsii Trel. loc. cit. 1927, not C.DC.

Page 404—The heading LOGANICACEAE should read LOGANIACEAE.

Page 418, line 23—*unita* should read *unitus.*

Page 439, line 10, delete "English."

Page 453, line 2 of caption—fungi should read sori.

Page 457, line 4—Transpose sentence beginning "Although" to last line on page 454.

Page 457, paragraph 5, line 6—fig. 6 should read fig. 7.

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Annals
of the
Missouri Botanical Garden

Volume XXXVII

1950

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GARDEN LIBRARY

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SHELVE IN STACKS

Volume XXXVII Number 1

Annals
of the
Missouri Botanical
Garden

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FEBRUARY, 1950

Flora of Panama. Part IV. Fascicle 1 (Piperaceae) . . . . . .
Robert E. Woodson, Jr., Robert W. Schery and Collaborators 1–120

PUBLISHED QUARTERLY AT GALESBURG, ILLINOIS,
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FLORA OF PANAMA

Part IV. Fascicle 1

PIPERACEAE[1]

By T. G. YUNCKER

Herbs, shrubs, or small trees, not infrequently repent or scandent, often with nodose stems, glabrous or pubescent, vascular bundles scattered; leaves mostly alternate, sometimes opposite or verticillate, simple, usually entire, ranging in size from less than 1 cm. up to 30–40 cm. or more long, often with glandular or pellucid dots; stipules lacking or present and commonly more or less adnate to the petiole; flowers very small, usually green, perfect or unisexual, in racemose or more commonly spike-like inflorescences, these usually somewhat fleshy, pedunculate, terminal or leaf-opposed, sometimes axillary or multiple on a common peduncle; the flowers mostly densely crowded, each in the axil of a usually peltate or subpeltate, sessile or stipitate, occasionally adnate or concave bract; perianth none; stamens usually 2–6, filaments mostly free, the anthers terminal, erect, 2-celled; ovary sessile or stipitate, 1-celled, 1-ovulate; fruit drupaceous, small.

The Piperaceae, one of the larger families of flowering plants, is pantropic in its distribution. Species are especially abundant in Latin America. They extend from the Keys of Florida through the West Indies, Mexico, and Central America, southward to Chile and Argentina. They occur in greatest number throughout northern South America from Brazil to Peru and northward to Panama and Costa Rica. Some species are widespread in their occurrence but each country has a rather large number of endemics. The total number of valid American species is unknown but unquestionably amounts to many hundreds and may approximate 2,000 or more.

A number of species of widespread distribution; e.g., *Piper aduncum, P. hispidum, P. marginatum,* and others appear to exhibit an infinite capacity of variation in minor characters of leaf size, shape, and indumentum. The extremes often appear quite distinct in themselves but study of large numbers of collections may reveal intergradations to such a degree that the extremes lose their seeming significance. The writer has been reluctant to maintain species or even varieties established by previous workers on such apparent variations when sufficient evidence indicates intergradations. It is probable that errors of judgment have been made but it is felt that such errors are on the side of conservatism. On this basis,

[1]Issued March 31, 1950.

a number of previously described species have been reduced to synonymy. At the same time, a number of novelties have been described as new to science. It is believed that with greater abundance of material, especially mass collections, and with correlated field study still further reductions may be in order. On the other hand, such studies may prove the validity of species which now appear to be the same.

Small collections had been made in Panama previous to 1800 especially by Née and by Haenke, and around the middle of the last century larger collections were prepared by Seemann, Fendler, Hayes, and others. However, collecting in Panama on an extensive basis did not get under way to any extent until after 1900.

Miquel, the great Dutch authority and monographer of the Piperaceae during the first part of last century, studied some of the earlier collections. Casimir DeCandolle, third in line of the great Swiss family of botanists, following Miquel's death, published in the DeCandolle 'Prodromus' in 1869 a monograph of the Piperaceae. Included in this publication were all of the species then known from Panama. Following this work, there appeared an almost continuous stream of papers by DeCandolle embodying the descriptions of hundreds of new species based on specimens sent to him by collectors as they explored farther and farther into botanically unknown areas. Following DeCandolle's death in 1918, Professor William Trelease, of the University of Illinois, undertook the study of the family, especially as it is represented in the Americas, and published a number of papers including the descriptions of many new species.

The earliest paper to deal exclusively with the Piperaceae of Panama was prepared by DeCandolle and published posthumously in 1920. This included the descriptions of a number of new species based on collections made by Pittier and by Maxon in the early part of the century. Subsequently, large collections were made by Standley, Killip, Piper, and others. From a study of this rather considerable accumulation of material, Trelease in 1927 presented a monographic study of the Panamanian Piperaceae which included 139 species and a number of varieties. Woodson and his associates at the Missouri Botanical Garden have more recently made extensive collections. These have also been studied by Trelease who has published more than 70 new species and a number of varieties based on this material. Thus, according to Trelease, more than 200 species are represented in Panama.

An attempt has been made in preparing the present paper to account for all species previously reported. Ninety-five species of *Piper*, 1 of *Ottonia*, 2 of *Pothomorphe*, 1 of *Sarcorhachis*, 1 of *Anderssoniopiper*, 72 of *Peperomia*, 22 varieties of *Piper* and 7 of *Peperomia*, making a total of 172 species and 29 varieties, are considered as valid in the present treatment.

For the present study the writer has had the loan of the collections at Gray Herbarium of Harvard University, University of Illinois, Missouri Botanical Garden, New York Botanical Garden, and the United States National Museum. In addition, he has also had the loan of a number of critical specimens from Kew. He had the use of notes made by Trelease during his studies of type material in

European herbaria and was also given a grant by the Research Grant Fund of DePauw University. For the loan of specimens and all other assistance given him, the writer expresses his thanks.

KEY TO GENERA*

a. Stigmas 2–5 (mostly 3–4); floral bracts various, often more or less pubescent; plants more or less woody, commonly shrubby or vine-like, or less frequently herbaceous.
  b. Inflorescence leaf-opposed.
    c. Inflorescence spicate; fruit sessile ..... 1. PIPER
    cc. Inflorescence racemose; fruit stipitate ..... 2. OTTONIA
  bb. Inflorescence axillary, spicate.
    c. Spikes several on a common peduncle ..... 3. POTHOMORPHE
    cc. Spikes one, or, if more than one, not on a common peduncle.
      d. Spikes solitary ..... 4. SARCORHACHIS
      dd. Spikes 2 (or more?), superposed, axillary ..... 5. ANDERSSONIOPIPER
aa. Stigmas 1 (may occasionally be cleft to simulate 2), stamens 2; floral bracts mostly round-peltate, glabrous; plants herbaceous, mostly comparatively small ..... 6. PEPEROMIA

1. PIPER Linnaeus

PIPER L. Gen. Pl. ed. 1. 333. 1737.

Shrubs or trees, occasionally subherbaceous, rarely scandent, often nodose; leaves alternate, simple, with rare exceptions entire, a few species peltate, frequently with one side attached to the petiole at the base several mm. lower than the other, smooth to rugose or bullate above and lacunose beneath, glabrous or sparsely to densely hairy, often scabrous, frequently sparsely to densely glandular-dotted, palmately nerved or more commonly pinnately nerved from the lower half or two-thirds, or throughout, usually somewhat venulose with finer cross-connecting and anastomosing nervules; petiole of various lengths, rarely lacking, commonly more or less vaginate-grooved at least at the base and often to the blade, the margins of the groove wing-margined, the wing very narrow or apparently lacking, or broad and conspicuous; spikes leaf-opposed, cylindrical or rarely globose or subglobose, 1–10 mm. or more thick and up to 50 cm. or more long; peduncle from less than 5 mm. up to several centimeters long; rachis commonly somewhat ridged between the flowers, the ridges low and smooth or papillate to fimbriate; flowers sessile and perfect (American species) or imperfect (Old World species); usually densely congested, in the axis of variously shaped bracts, the bracts sometimes glabrous but more commonly pilose or fimbriate; stamens 2–5; ovary 1, glabrous or sometimes papillate or pubescent; stigmas 2–4, rounded to filiform, sessile or on a short and thick to elongated and slender style; fruit variously shaped, one-seeded, drupe-like, with a thin pericarp and somewhat hardened endocarp.

PRIMARY KEY TO SPECIES OF PIPER

a. Ovary and fruit stylose ..... I. Spp. 1–18 (pp. 5–14)
aa. Ovary and fruit not stylose.
  b. Leaves scarcely peltate.
    c. Leaves palmately nerved, or plinerved within the lowermost 5 mm. ..... II. Spp. 19–25 (pp. 15–20)
    cc. Leaves pinnately nerved.
      d. The principal branches of the midrib arising from somewhat below the middle to the upper third of the blade.

*All keys in this paper are to be considered as artificial.

e. Leaves mostly 20–25 cm. or more long × 10–20 cm. or more wide, base equi- or unequilaterally lobed (shallowly so in a few species) ..... III. Spp. 26–34 (pp. 20–26)
ee. Leaves mostly smaller or, if large, not lobed at the base..... IV. Spp. 35–82 (pp. 30–60)
dd. The midrib more or less equally branched to the upper fourth or throughout ..... V. Spp. 83–93 (pp. 61–69)
bb. Leaves distinctly peltate ..... VI. Spp. 94–96 (pp. 70–71)

I. KEY TO SPECIES HAVING STYLOSE OVARIES AND FRUIT

(In a few species included here the styles may be very short or easily deciduous. Such questionably stylose species have been also included in the non-stylose section of the key.)

a. Leaves rugose-bullate ..... 1. P. PESARESANUM
aa. Leaves not rugose-bullate.
b. Leaves peltate ..... 95. P. MAXONII
bb. Leaves not peltate.
c. Spikes 15–20 cm. or more long; leaves 10 × 20 cm. or more; styles short.
d. Petioles, twigs, etc. more or less warty-verrucose ..... 30. P. IMPERIALE
dd. Petioles, twigs, etc. not warty-verrucose.
e. Twigs glabrate; nerves 6–8 on each side
f. Leaves elliptic, base oblique, cordate-auriculate ..... 2. P. ALBOPUNCTULATISSIMUM
ff. Leaves ovate, base not oblique or auriculate ..... 34. P. PITTIERI
ee. Twigs densely brown-hairy; nerves 5–6 on each side ..... 31. P. TARDENS
cc. Spikes and leaves much smaller.
d. Spikes mostly 3 cm. or more long when mature.
e. Leaves pinnately nerved throughout; plants entirely glabrous; fruit tetragonous; bracts cupulate, glabrous ..... 3. P. DARIENENSE
ee. Leaves pinnately nerved below the upper third (or sometimes throughout in *P. phytolaccaefolium*).
f. Young twigs and/or leaves hairy.
g. Spikes 6–8 cm. long; peduncle 1.5–2 cm. long ..... 4. P. LINCOLNENSE
gg. Spikes 3–4 cm. or less long; peduncle 0.5–1 cm. long.
h. Leaves ovate, 7–12.5 cm. wide; twigs retrorsely hirtellous ..... 5. P. PERVENOSUM
hh. Leaves lance-elliptic, 3.5–5 cm. wide; twigs villous ..... 6. P. PERULIGERUM
hhh. Leaves elliptic-obovate or obovate, 7–12 cm. wide ..... 7. P. EXIGUICAULE
ff. Entirely glabrous.
g. Leaves ovate, base rounded; spikes 5 cm. or more long ..... 8. P. CRASSINERVIUM var. TOCOTANUM
gg. Leaves not ovate, base acute to acuminate.
h. Leaves lance-elliptic; spikes 2–4 cm. long ..... 9. P. PHYTOLACCAEFOLIUM
hh. Leaves obovate, strongly revolute ..... 10. P. MACROPUNCTATUM
dd. Spikes mostly 2 cm. or less long when mature.
e. Leaves with 6–8 main lateral nerves.
f. Leaves 10 cm. or more wide, nerves beneath puberulent ..... 11. P. LATIBRACTEUM
ff. Leaves less than 5 cm. wide, nerves beneath glabrous ..... 12. P. CANDELARIANUM
ee. Leaves with 3–5 main lateral nerves.
f. Leaf base 5–10 mm. shorter on one side, glabrous ..... 13. P. MAGNANTHERUM
ff. Leaf base essentially equilateral, or if unequal more or less pubescent.
g. Young twigs and/or leaves hairy.
h. Leaves more or less long-ciliate, base acute ..... 14. P. GARAGARANUM
hh. Leaves not ciliate, base more or less cordulate.
i. Twigs, petioles, etc. minutely hirtellous ..... 5. P. PERVENOSUM
ii. Twigs, etc. densely villous.
j. Leaves about three times longer than wide, oblong-lanceolate ..... 15. P. PUBISTIPULUM
jj. Leaves about 2 times longer than wide, elliptic ..... 16. P. COLON-INSULAE

gg. Young growth glabrous.
h. Leaves mostly 6 cm. or more wide.
i. Leaves broadly elliptic, abruptly short-acuminate, subrugose..... 17. P. DISTIGMATUM
ii. Leaves ovate, gradually acuminate, not rugose..... 18. P. DAVIDSONII
hh. Leaves mostly narrower..... 9. P. PHYTOLACCAEFOLIUM

1. PIPER PESARESANUM C.DC. in Engl. Bot. Jahrb. 40:247. 1908, as *petaresanum*, obviously an error.

Piper fluvii-initii Trel. in Ann. Mo. Bot. Gard. 27:291. 1940.

A shrub or small tree, 3–8 m. tall, nodose; upper internodes rather short, thick, subreflexed-hirtellous with an intermixture of scattered long hairs; leaves elliptic- to round-ovate, 5–11 cm. wide × 13–17 cm. long, apex sharp-acuminate, base rounded, subinequilaterally obtuse, one side 1–2 mm. shorter, bullate-lacunose, pinnately nerved from the lower half, the nerves about 6 or 8 on each side, rusty-villous above, at least along the nerves, rather densely so beneath, especially along the nerves, with a mixture of long and short hairs, margin ciliate, drying firm, dark, opaque; petiole 10–20 plus 1–2 mm.[2] long, villous, vaginate and narrowly winged toward the base; spikes 8–10 mm. thick × 9–13 cm. long; peduncle stout, 1–2 cm. long, villous; bracts oblong-subligulate, pilose to near the subacute, curved apex; fruit subcylindrical, glabrate, stigmas 3, elongated, recurved on a moderate or short, somewhat sparsely hispid or glabrate style.

Western Colombia and Panama, commonly at rather high altitudes.

CHIRIQUÍ: trail from Cerro Punta to headwaters of Río Caldera, alt. 2250–2500 m., *Allen 1445;* Bajo Chorro, Boquete District, alt. 2100 m., *Davidson 204.*

This species rather closely resembles *P. lacunosum* of western South America but differs in the type of pubescence, shape of the bracts, and more elongated fruits. The Chiriquí specimens agree in all respects with those seen from South America.

2. PIPER ALBOPUNCTULATISSIMUM Trel. in Ann. Mo. Bot. Gard. 27:287. 1940.

A somewhat nodose shrub, 4 m. tall; upper internodes glabrous, sparingly warty-papillate; leaves elliptic, apex acute, base obliquely cordate-auricled, one side about 5 mm. shorter at the petiole, the larger side about equaling the petiole, about 18 cm. wide × 28–30 cm. long, pinnately nerved from below the upper third, the nerves 6–8 on each side, submarginally loop-connected and with numerous cross-connecting and anastomosing nervules, glabrous above, the nerves beneath puberulent or crisp-pubescent, marginal ciliation lacking, sparsely yellow-glandular-dotted on both sides, microscopically white-dotted above when dry, drying rather firm, subtranslucent; petiole 45 plus 5 mm. long, winged-vaginate to near the blade, sparsely warty; spikes 5 mm. thick × 25 cm. long; peduncle

[2] The base of the blade in many species of *Piper* is unequal on the two sides with one side somewhat shorter at the petiole. The petiolar length is given plus the difference in length between the two sides.

about 4 cm. long; bracts triangular-subpeltate, ciliate, the pedicel broad, concave; stigmas 3, linear, on a short, stout style.

Known only from the following locality.

COCLÉ: north rim of El Valle de Antón, alt. 600–1000 m., *Allen 1652*.

3. PIPER DARIENENSE C.DC. in DC. Prodr. 16[1]:374. 1869.

Ottonia glaucescens Miq. in Seem. Bot. Voy. Herald, 200. 1854, not *Piper glaucescens* Jacq.
Piper dariense C.DC. in Candollea 1:168. 1923.
Piper laxispicum Trel. in Contr. U. S. Nat. Herb. 26:24. 1927.
Piper laxispicum var. *latifolium* Trel. loc. cit. 1927.
Piper Permari Trel. in Ann. Mo. Bot. Gard. 27:295. 1940.
Piper fagopyricarpum Trel. loc. cit. 28:426. 1941.

A glabrous shrub, mostly scarcely 0.5 m. tall; stems simple or occasionally branched, 2–3 mm. thick, somewhat finely striate, greenish; leaves oblong-elliptic, subovate or lance-elliptic, 3–7 or sometimes 8 cm. wide × 12–19 cm. long, apex attenuately sharp-acuminate, base narrowed, subequilaterally acute or rounded and obtuse, minutely auriculate at the petiole, pinnately nerved throughout, the midrib rather prominent beneath, the lateral nerves slender, 6–9 on each side, divergent and submarginally loop-connected, drying green above, paler and subglaucous beneath, membranous, translucent; petiole mostly scarcely 5 mm. long, longitudinally striate, scarcely vaginate at the very base; spikes 3–5 mm. thick × 3–5 cm. long when mature; peduncle about 5 mm. long; rachis smooth or obscurely papillate; bracts cupulate, glabrous; fruit mostly exserted, free, globose-tetragonous, smooth or obscurely papillate, stigmas short, 3–4, on a short, stout style.

Panama and northern Colombia.

BOCAS DEL TORO: upper Changuinola River, *Permar s. n.*; vicinity of Chiriquí Lagoon, *von Wedel 1042*. CHIRIQUÍ: vicinity of Puerto Armuelles, alt. 0–75 m., *Woodson & Schery 852*. CANAL ZONE: Barro Colorado Island, Gatún Lake, *Standley 31375; Mexia 6551; Bailey & Bailey 88*. PANAMÁ: Indio, Madden Lake, *Miller 2065*—leaves maximum size, as described. SAN BLAS: forests around Puerto Obaldía, alt. 0–50 m., *Pittier 4288*.

The type specimen did not have a sufficiently matured spike to show the characters of the fruit, which are significant in this species. The description of the vegetative characters, however, agrees in all respects with the other specimens included here. It was reported by Seemann as being used by the Indians for stupeyfing fish. Mexia made the same report for the specimen she collected on Barro Colorado Island.

4. PIPER LINCOLNENSE Trel. in Field Mus. Nat. Hist. Bot. Ser. 18:347. 1937.

A shrub (?); flowering internodes moderately slender and short, obscurely retrorsely hirtellous on one side, the other side papillate glabrescent; leaves broadly elliptic or ovate-elliptic, apex short-acuminate, base slightly inequilaterally cordulate, 7.5–10.5 cm. wide × 16–20 cm. long, pinnately nerved from below the upper third, the nerves about 6 on each side, rather prominent beneath, glabrous above, glandular-dotted and crisp-pubescent beneath, especially along the nerves, not ciliate, drying dull, papery, translucent; petiole 1.5–2 cm. long, rather densely

reflexed-hirtellous, vaginate to the blade; spikes 3–4 mm. thick × 6–8 cm. long, peduncle 1.5–2 cm. long, thinly and obscurely hirtellous; bracts triangular, the pedicel broad and concave, glabrous; fruit depressed, slightly flattened laterally with the rachis, stigmas 3, slender, on a short style.

Known only from Lincoln Creek, Bocas del Toro.

BOCAS DEL TORO: Lincoln Creek, Changuinola Valley, *Dunlap 408*.

The broadly elliptic leaves, pubescent beneath, and stylose fruits characterize this species.

5. PIPER PERVENOSUM C.DC. in Candollea 1:268. 1923, name only; Schroeder, in Candollea 3:137. 1926.

A shrub; flowering internodes short, moderately slender, retrorsely hirtellous; leaves ovate, apex gradually acute, base subequilateral, rounded, obtuse or subcordulate, 7–12.5 cm. wide × 13–18 cm. long, glabrous on both sides or with the nerves beneath obscurely and minutely hirtellous, pinnately nerved from the lower half or slightly above, the nerves 3 or 4 on each side, with shorter intermediates, and minor lateral nerves to near the apex, nervules very numerous and closely spaced as seen by transmitted light, glandular-dotted, the glands comparatively large, drying gray-green, firm, translucent; petiole 5–20 mm. long, stout, vaginate-winged to the blade, retrorsely hirtellous; spikes 3–4 mm. thick × 3 cm. long; peduncle 5–10 mm. long, hirtellous; bracts triangular-lunulate, papillate; ovary subglobose, stigmas small, on a short style.

Known only from the following locality.

SAN BLAS: San Blas coast, high hills back of Puerto Obaldía, alt. 50–200 m., *Pittier 4302*

The gray-green twigs and ovate, finely venulose leaves are distinctive features of this species.

6. PIPER PERULIGERUM Trel. in Ann. Mo. Bot. Gard. 27:295. 1940.

Small and suffruticose; twigs, petioles and leaves at first rusty subtomentose-villous; internodes short and rather slender; leaves lance-elliptic, apex long-attenuate, base obliquely cordulate, one side 2–3 mm. longer, 3.5–5 cm. wide × 11–14 cm. long, pinnately nerved from the lower half, the nerves 3–5 on each side, with strong cross-connecting-anastomosing nervules, becoming slightly pouched between veins, the midrib above moderately pubescent, subvillous beneath, the nerves rather strongly so, the hairs staring and of various lengths, the longest nearly 1 mm. long, drying papery, translucent; petiole scant 3 plus 2–3 mm. long, densely villous; spikes 3 mm. thick × 2.5 cm. long; peduncle 3 mm. long; stigmas on a short style.

Known only from the following locality.

BOCAS DEL TORO: Isla de Colón, *Woodson, Allen & Seibert 1939*.

The above description is drawn largely from the type description by Trelease inasmuch as the fragment at Illinois consists of two leaves only. Trelease indicated that the type is at the Missouri Botanical Garden but it has not been seen by the writer.

7. Piper **exiguicaule** Yuncker, sp. nov.

Frutex, 30 cm. altus; foliis obovatis vel elliptico-obovatis, apice subacutis, basi subaequilateralibus, ad petiolum abrupte acutis, a tertio supero deorsum pinnatim venosis, venis utrinque ca. 6, supra dissite villosis, subtus ad venas crispe vel adpresse pubescentibus, sat obscure glanduloso-punctatis; petiolo 2 cm. vel ultra longo; spicis, ut adsunt, 3 mm. crassis, 3.5 cm. longis; pedunculo 2.5 cm. longo; bracteis triangulari-subpeltatis, conferte pallido-fimbriatis; ovario subgloboso, stylo brevi; stigmatibus 3, rotundatis.

Shrub, 30 cm. tall; stem sparsely pubescent (?); leaves obovate or elliptic-obovate, apex acutish, base subequilateral and abruptly acute at the petiole, 7–12 cm. wide × 12–19 cm. long, pinnately nerved below the upper third, the nerves about 6 on each side, with prominent cross-connecting-anastomosing nervules, sparsely villous above, the nerves beneath crisp- or appressed-pubescent, rather obscurely glandular-dotted, drying papery, translucent, finely pellucid-dotted; petiole up to 2 cm. or more long, vaginate toward the base (?); spikes as yet young, 3 mm. thick × 3.5 cm. long; peduncle 2.5 cm. long, sparsely pubescent; bracts triangular-subpeltate, densely pale-fringed; ovary subglobose, stigmas 3, rounded, on a rather short, stout style; fruit not developed.

Known only from the one collection.

Bocas del Toro: Fish Creek, Apr. 9, 1941, *von Wedel 2187* (Herb. Missouri Bot. Gard., type).

The type specimen is rather poor and fragmentary but it does not appear to agree with any other known species. The very small plants, obovate leaves, densely fringed bracts, and stylose ovaries are distinctive characters.

8. Piper crassinervium H.B.K. var. **tocotanum** (C.DC.) Yuncker, comb. nov.

Piper exserrens (Miq.) C.DC. var. *tocotanum* C.DC. in Ann. Conserv. & Jard. Bot. Genève 21:239. 1920.

Piper papyraceum Trel. in Contr. U. S. Nat. Herb. 26:31. 1927.

Piper novae-helveticae Trel. in Ann. Mo. Bot. Gard. 27:294. 1940.

An essentially glabrous shrub or small tree, 2–5 m. tall; upper internodes comparatively short but soon lengthening, glabrous; leaves ovate, 5–14 cm. wide × 13–23 cm. long, apex acuminate, base rounded, obtuse or in large leaves sometimes shallowly cordate, equilateral or with one side slightly shorter, abruptly acute

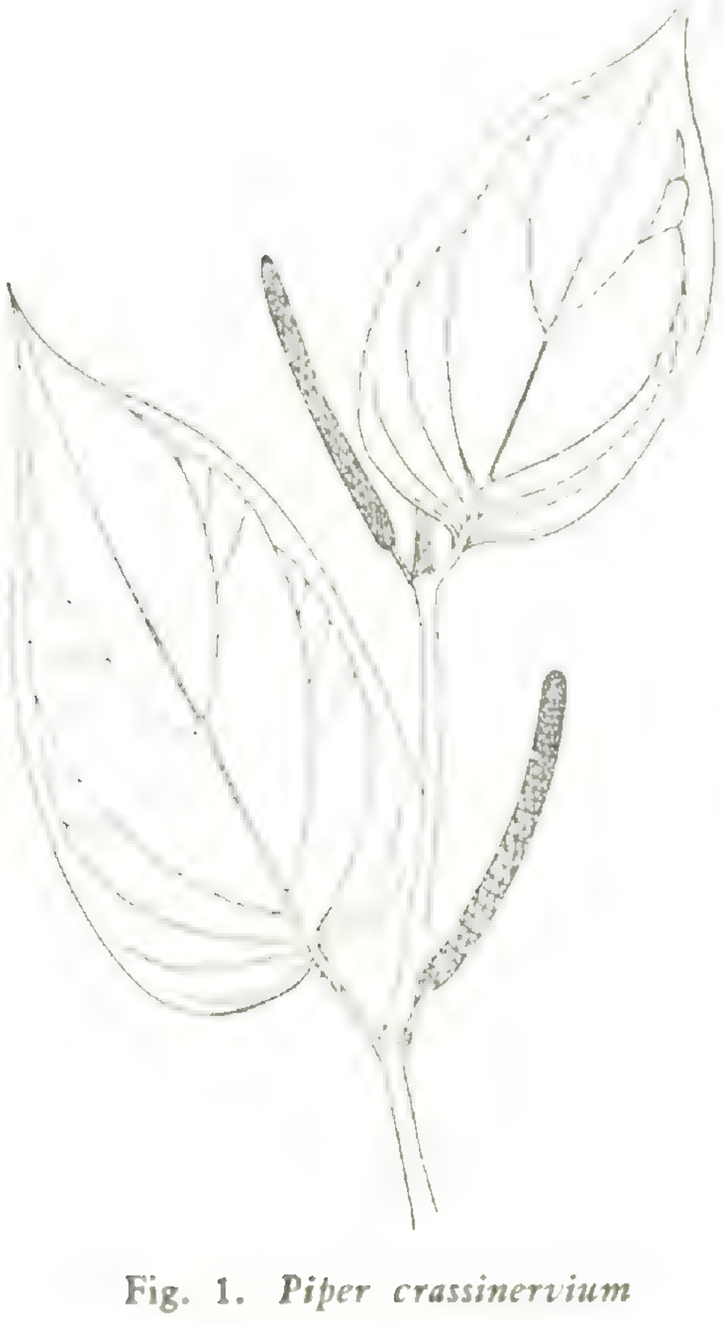

Fig. 1. *Piper crassinervium* var. *tocotanum*

at the petiole, pinnately nerved from below the middle, the nerves 4 or 5 on each side, prominent beneath, glabrous or at most only sparsely minutely puberulent along the nerves, drying firm, translucent; petiole about 15 mm. long, vaginate and narrowly winged to the middle or above; spikes 5–7 mm. thick × 12–15 cm. long when mature; peduncle stout, 5–15 mm. long, pubescent; bracts rounded- or triangular-subpeltate, marginally fringed, zonately arranged; fruit rounded, glabrate, stigmas 3, recurved, on a rather short style.

Venezuela, Colombia, and Panama; the species Colombia and Ecuador.

CHIRIQUÍ: vicinity of "New Switzerland," central valley of Río Chiriquí Viejo, alt. 1800–2000 m., *Allen 1359, 1416;* forests around El Boquete, alt. 1000–1300 m., *Pittier 3023.*

No significant difference has been found by means of which the Panamanian specimens can be distinguished from those from South America.

9. PIPER PHYTOLACCAEFOLIUM Opiz in Presl, Reliq. Haenk. 151. 1830.

Piper brevispicatum Opiz, loc. cit. 151, *pl. 28.* 1830.
Artanthe heterophylla Miq., Syst. Pip. 502. 1844.
Artanthe brevispicata Miq., loc. cit. 508. 1844.
Artanthe phytolaccaefolia Miq., loc. cit. 534. 1844.
Peltobryon phytolaccaefolium Presl, Epim. Bot. 224. 1849.
Piper singulare C.DC. in Jour. Bot. 4:161. 1866.
Piper amphoricarpum Trel. in Contr. U. S. Nat. Herb. 26:29. 1927.
Piper simulans Trel. in Field Mus. Nat. Hist. Bot. Ser. 18:361. 1937.

A glandular-granular shrub, 1–2 m. tall, glabrous or obscurely and transiently puberulent; twigs rather slender; leaves lance- or oblong-elliptic, 3–6 cm. wide × 10–13 cm. long, or occasionally up to 8 × 19 cm., apex acuminate, base acute to cuneate, mostly equilateral, glandular-dotted, often strongly so, pinnately nerved throughout or some leaves from below the upper third, the nerves 4, or in large leaves 5–6 on each side, mostly scarcely ciliate; petiole 5–10 mm. long, vaginate at the base; spikes 5 mm. thick × 2–4 cm. long; peduncle 5–20 mm. long, glabrate or very sparsely hirtellous; bracts triangular- or rounded-subpeltate, marginally fringed; fruit globose, stigmas 3, small, on a short subulate style.

Colombia, Ecuador, and Panama.

PANAMA: without definite locality, *Née 363, 364, 367.* BOCAS DEL TORO: Changuinola Valley, *Dunlap 459.* CHIRIQUÍ: Boquete District, Boquete, alt. 1140 m., *Davidson 619;* along Río Caldera, south of El Boquete, alt. 1250 m., *Killip 3611.*

No significant differences have been discovered between the Panamanian specimens cited here and those which have been studied from South America. Those from Panama, however, are, so far as seen, less conspicuously glandular-dotted than are those of South America. A specimen collected by Née without definite locality indicated has the leaves ciliate and with a few scattered long hairs on the upper surface.

10. Piper **macropunctatum** Yuncker, sp. nov.

Fig. 2. *Piper macropunctatum*

Frutex, ca. 0.5 m. altus, dissite hirtulus; internodiis usque ad 6 cm. longis, obvie conferte glandulosis; foliis elliptico-obovatis, apice obtusis vel abrupte brevi-acutis, basi inaequilateraliter acutis, latere altero ca. 2 mm. breviore, utrinque glabratis vel subtus ad basem dissite pubescentibus, a medio laminae deorsum pinnatim venosis, venis utrinque 5, utrinque conferte glanduloso-punctatis, margine revolutis; petiolo 2–4 cm. cum 2 mm. longo; basi vaginato; bracteis triangulari-lunato-subpeltatis; ovario ovoideo glanduloso, stylo brevi, crasso, subalato, stigmatibus parvis.

A small, essentially glabrous shrub, about 0.5 m. tall; stem unbranched, internodes up to 6 cm. long, strongly glandular-dotted; leaves elliptic-obovate, apex obtuse or abruptly short-acute, base inequilaterally acute, one side about 2 mm. shorter, 6–8.5 cm. wide × 13–15 cm. long, glabrous on both sides or sparsely pubescent near the base beneath, pinnately nerved from the lower half, the nerves 5 on each side, with cross-connecting-anastomosing nervules, submarginally loop-connected, strongly glandular-dotted on both sides, drying rather thin, translucent, pellucid-dotted, revolute; petiole 2–4 cm. plus 2 mm. long, glabrous or sparsely pubescent, vaginate near the base; spikes 3 mm. thick × 2.5 cm. or more long; bracts triangular-lunate-subpeltate, glabrous (?); ovary glandular, ovoid, with a short, stout, subulate style, stigmas small, sessile.

Known only from the type locality.

BOCAS DEL TORO: Pumpkin River, July 28, 1941, *von Wedel 2561* (Herb. Missouri Bot. Gard., TYPE).

The small, simple, glabrous plants, strongly glandular-dotted with comparatively large dots, obovate, revolute leaves, and pointed ovary distinguish this species. The only spike present on the type specimen is fragmentary and young.

11. Piper latibracteum C.DC. in Smiths. Misc. Coll. 71^{6}:5. 1920.

A shrub, about 1 m. tall; flowering internodes moderately stout and short, glabrous; leaves broad-elliptic, apex gradually acute, base narrowed, obtuse or slightly cordulate, one side 1–2 mm. shorter, 11–14 cm. wide × 20–24 cm. long, pinnately nerved below the upper third, the nerves 7–8 on each side, with intermediates and slender cross-connecting and anastomosing nervules, glabrous above, the nerves beneath puberulent, somewhat rugose, glandular-dotted, drying subglossy and green above, paler beneath, papery, translucent; petiole 15–20 plus 1–2 mm. long, vaginate and narrowly winged to the blade; spikes 8 mm. thick × 2 cm. long, apiculate; peduncle stout, scarcely 10 mm. long; bracts triangular-lunate,

glabrous, or marginally papillate, pedicel broad, concave; ovary glabrous, stigmas 2, recurved, on a short, stout style.

Southern Panama.

DARIÉN: Boca de Pauarandó, Sambú River, alt. 20 m., *Pittier 5588;* Cañi-Cuasi Trail, Chepigana Dist., alt. 900 m., *Terry & Terry 1441;* alt. 1650 m., *Terry & Terry 1581.*

The numerous nerves, puberulent beneath, short, thick, apiculate spikes, and stylose ovaries distinguish this species.

12. PIPER CANDELARIANUM C.DC. in Linnaea 37:357. 1872.

Piper globosum C.DC. loc. cit. 340. 1872 not Poir. 1804.
Piper psilocladum C.DC. in Bull. Soc. Bot. Belg. 30^1:211. 1891.

Scandent shrub, glabrous; flowering internodes rather slender and short, red-granular; leaves lance-elliptic or the lower subovate, apex gradually acute, base subequally acute or one side slightly shorter than the other, 2.5–4 cm. wide × 8–12 cm. long, pinnately nerved throughout, the nerves mostly 6–7 on each side, with rather obscure intermediates and cross-connecting nervules, drying thin but firm, translucent, prominently yellow- or red-glandular-dotted on both sides; petiole scarcely 1 cm. long, vaginate toward the base; spikes 4–8 mm. thick × 1.5–2.5 cm. long, mucronate; peduncle slender, about 1 cm. long, eventually recurving; bracts triangular-subpeltate, sparingly very short-fringed on the upper margin; fruit rather large, globose, attenuate into a short, stout style, conspicuously glandular roughened, glabrous, stigmas 3.

Costa Rica and adjacent Panama.

BOCAS DEL TORO: Old Bank Island, vicinity of Chiriquí Lagoon, *von Wedel 1994.*

The short, thick styles, short spikes, glandular twigs, and pinnately nerved leaves are distinctive characters of this species. It resembles *P. cumaralense* of Colombia to some extent but differs because of its completely glabrous twigs and leaves and with the nerves of the leaves not submarginally loop-connected as in that species.

13. PIPER MAGNANTHERUM C.DC. in Smiths. Misc. Coll. 71^6:16. 1920.

A glabrous, strongly red-glandular shrub (?); flowering internodes short and slender; leaves lance-elliptic-oblong, apex acuminate, base obliquely acute, one side 5–10 mm. shorter, 3.5–5 cm. wide × 12–15 cm. long, pinnately nerved from the lower half, the nerves 4 or 5 on each side, or with additional lateral nerves to the upper fourth, with few cross-connecting nervules, rather loosely ciliate toward the apex, drying thin, translucent; petiole 5–10 plus 5–10 mm. long, or on lower leaves up to 2 cm., vaginate at the base; spikes as yet young, 2–3 mm. thick × 1.5 cm. long, mucronate, peduncle 5–8 mm. long; bracts triangular-subpeltate, marginally pale-ciliate; ovary ovoid, narrowing into a short, stout style, stigmas 3, small, short.

Known only from the following locality.

DARIÉN: Cerro de Garagará, Sambú basin, southern Darién, alt. 500–974 m., *Pittier 5666*.

The densely red-glandular leaves, twigs, etc., strongly inequilateral base of the leaves, and stylose ovaries distinguish this species. It resembles *P. phytolaccaefolium* in many respects but differs because of the inequilaterally based leaves, and conspicuous red-glands.

14. PIPER GARAGARANUM C.DC. in Smiths. Misc. Coll. 71^6:15. 1920.

A shrub; flowering internodes moderately slender, rather short, moderately to sparsely loosely villous; leaves lance-elliptic, apex sharp-acuminate, base equilateral and obtusish, or more commonly inequilateral and acute with one side about 2 mm. shorter, 4.5–7 cm. wide × 13–17 cm. long, pinnately nerved from below the middle, the nerves 3–4 or 5 on each side, with rather open, cross-connecting-anastomosing nervules, loosely long-villous, especially along the nerves beneath, somewhat long-ciliate, glandular-dotted beneath, drying rather thin and papery, translucent; petiole 20 plus 2 mm. long on lower leaves and vaginate-winged to about the middle, reduced upward, villous; spikes 3 mm. thick × 15–18 mm. long; peduncle about 5 mm. long, villous; bracts small, concave, short-ciliate along the concave margin; ovary ovoid, narrowing into a short, stout style, stigmas rather short, recurved.

Darién Province.

DARIÉN: foothills of Garagará, Sambú basin, alt. 30–500 m., *Pittier 5618;* Chepigana Dist., Caña-Cuasi Trail (Camp 2), alt. 600 m., *Terry & Terry 1432*.

The short spikes, and thinly long-villous and ciliate leaves distinguish this species.

15. PIPER PUBISTIPULUM C.DC. in Smiths. Misc. Coll. 71^6:5. 1920.

Piper pubistipulum var. *eustylosum* Trel. in Contr. U. S. Nat. Herb. 26:28. 1927.

A small shrub, 1 m. tall; upper internodes short, densely retrorsely hirsute; leaves oblong-lanceolate, apex gradually rather long-acuminate, base somewhat narrowed, cordulate, one side 2–3 mm. shorter, glabrous above except for the midrib which is pubescent near the base, pubescent beneath with the nerves hirsute, 5–6 cm. wide × 15–19 cm. long, pinnately nerved from the lower half, the nerves 4 on each side, raised beneath, with cross-connecting and anastomosing nervules, sparsely glandular-dotted beneath, smooth or subrugose, drying firm, translucent; petiole stout, 6–8 plus 2 mm. long, densely hairy, deeply vaginate to the blade; spikes 3–4 mm. thick × 2 cm. long, mucronate; peduncle 5 mm. long, hirsute; bracts triangular-lunate, glabrous, pedicel broad, cupulate; ovary narrowed abruptly into a short, thick style, stigmas 2, recurved.

Central Panama.

CANAL ZONE: Barro Colorado Island, Gatún Lake, *Standley 31364;* hills around the Agua Clara Reservoir, near Gatún, alt. 20–30 m., *Pittier 2661*. PANAMÁ: Indio, *Miller 2078*.

The densely pubescent stems, oblong-lanceolate leaves, pubescent beneath and with somewhat inequilateral, cordulate bases, short spikes, and stylose fruits distinguish this species. The spike on the type of var. *eustylosum* is so young that it is not possible to determine the style character. The specimen agrees so well otherwise that it is believed that it is same as the species.

16. PIPER COLON-INSULAE Trel. in Ann. Mo. Bot. Gard. 27:290. 1940.

A shrub, 2 m. tall; upper internodes relatively slender, densely dingy-villous; leaves elliptic, apex acute or short-acuminate, base inequilaterally cordulate, margins subequal at the petiole, 5–8.5 cm. wide × 13–16 cm. long, glabrous above or the midrib with a few hairs at the very base, villous beneath, at least along the nerves, pinnately nerved below the upper third, the nerves about 5 on each side, with numerous cross-connecting-anastomosing nervules, drying papery, translucent; petiole 1–1.5 cm. long, densely dingy-villous, vaginate to the blade; spikes 5 mm. thick × 2.5–3 cm. long; peduncle 8 mm. long, subhirsute; bracts narrowly triangular-lunate, glabrous; fruit subquadrangular-oblong, stigmas on a very short style.

Known only from the following locality.

BOCAS DEL TORO: Isla de Colón, alt. 25–75 m., *Woodson, Allen & Seibert 1934.*

17. PIPER **distigmatum** Yuncker, sp. nov.

Frutex (?) vel arbuscula glabratus 2–3 m. altus; internodiis floriferis modice brevibus gracilibusque; foliis late ellipticis, apice abrupte breviter acuminatis, basi obtusis vel ad petiolum abrupte subacutis, rugosis, infra medium pinnatim venosis, venis utrinque 5, subtus prominentibus, rubro-glanduloso-punctatis; petiolo 1.5–2.5 cm. longo, ad laminam vaginato; spicis 5–8 mm. crassis, 1.5–2.2 cm. longis apiculatis; pedunculo ca. 1 cm. longo; bracteis triangulari-lunatis glabratis; drupa subglobosa, stigmatibus binis ligulatis recurvis, stylo sat longo crasso subulato fultis.

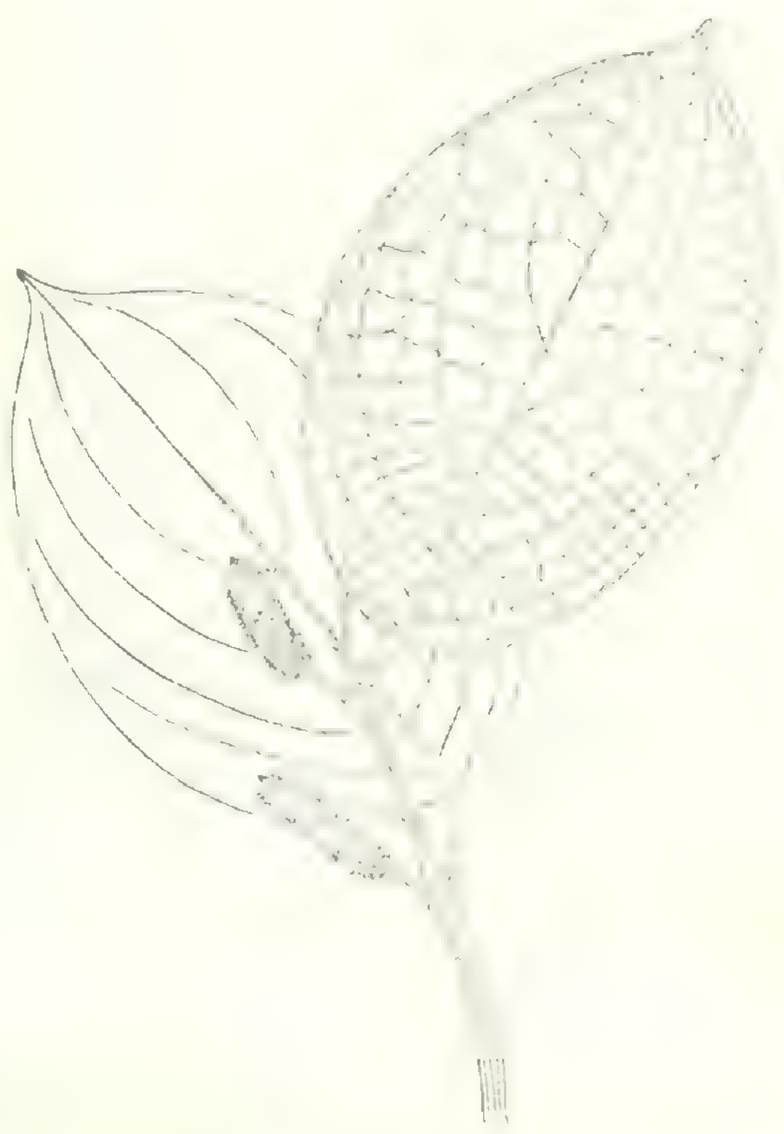

Fig. 3. *Piper distigmatum*

A glabrous shrub (?) or small tree, 2–3 m. tall; flowering internodes moderately short and slender; leaves broadly elliptic, apex abruptly short-acuminate, base rounded, obtuse or abruptly subacute at the petiole, 8–9.5 cm. wide × 14–17 cm. long, rugose, pinnately nerved from below the middle, the nerves 5 on each side, prominent beneath, not branched but with slender cross-connecting and anastomosing nervules, red-glandular-dotted, especially on the lower surface, drying firm, translucent; petiole 1.5–2.5

cm. long, vaginate to the blade; spikes 5–8 mm. thick × 1.5–2.2 cm. long, apiculate; peduncle about 1 cm. long; bracts triangular-lunate, glabrous, pedicel broad, curved; fruit subglobose, stigmas 2, ligulate, recurved, on a rather long, stoutish, subulate style.

Known only from the type locality.

CHIRIQUÍ: Boquete Region, Cerro Horqueta, cloud forest, alt. 1950 m., April 17, 1940, *von Hagen & von Hagen 2009* (Herb. Missouri Bot. Gard., TYPE); April 27, 1940, *von Hagen & von Hagen 2058*.

The broadly elliptic, somewhat rugose leaves, and bistigmatic, rather long-styled fruit distinguish this species. It differs from *P. Davidsonii* because of the shape of the larger, rugose, more abruptly acuminate leaves, 5-nerved on each side.

18. PIPER **Davidsonii** Yuncker, sp. nov.

Frutex parvus glaber; internodiis superis sat brevibus gracilibusque; foliis ovatis vel elliptico-ovatis, apice acuminatis, basi rotundatis ad petiolum abrupte acutis, infra medium pinnatim venosis, venis utrinque 4, manifeste rubro-glanduloso-punctatis; petiolo ca. 1.5 cm. longo, ad laminam vaginato; spicis, ut adsunt, 5 mm. crassis, 1 cm. longis; pedunculo 1 cm. longo; bracteis triangulari-subpeltatis, glabratis; ovario globoso (?), stigmatibus 2, stylo longo fultis.

A small, glabrous shrub, 1–2 m. tall; upper internodes rather short and slender; leaves ovate or elliptic-ovate, apex acuminate, base rounded, abruptly short-acute at the petiole, 6–7.5 cm. wide × 14–16 cm. long, pinnately nerved from below the middle, the nerves 4 on each side or with a very slender fifth nerve at the base in large leaves, strongly red-glandular-dotted, especially beneath, green above, pale beneath, drying firm, translucent; petiole about 1.5 cm. long, vaginate to the blade; spikes, as represented, 5 mm. thick × 1 cm. long; peduncle 1 cm. long; bracts triangular-subpeltate, glabrous, the pedicel broad, concave, papillate; ovary globose (?), stigmas 2, on an elongated style.

Known only from the type locality.

CHIRIQUÍ: Bajo Chorro, Boquete District, alt. 1800 m., Feb. 15, 1938, M. *E. Davidson 285* (Herb. Missouri Bot. Gard., TYPE).

II. KEY TO SPECIES WITH PALMATELY NERVED LEAVES

(The nerves may coalesce within the lowermost 5 mm.)

a. Fruit papillate, with a prominent, glabrous, apical disc ..... 19. P. RETICULATUM
aa. Fruit lacking any evident apical disc.
  b. Leaf base cordate.
    c. Leaves 9- to 11-nerved ..... 20. P. MARGINATUM
    cc. Leaves 5-nerved ..... 21. P. ARISTOLOCHIAEFOLIUM
  bb. Leaf base rounded or narrowed, scarcely cordate, leaves more or less elliptic.
    c. Leaf base inequilateral with one side about 2 mm. shorter; flowers approximated.
      d. Petiole vagina margin glabrous; leaves lanceolate, 3-nerved ..... 22. P. HUMORIGAUDENS
      dd. Petiole vagina margin ciliate; leaves lance-elliptic, 5-nerved ..... 23. P. CONVERSUM
    cc. Leaf base essentially equilateral, 5- to 7-nerved.
      d. Flowers distant; bracts glabrous ..... 24. P. PINOGANENSE
      dd. Flowers more compact; bracts papillate-pilose ..... 25. P. MEDIUM

19. PIPER RETICULATUM L. Sp. Pl. 1:29. 1753.

Piper smilacifolium H.B.K. Nov. Gen. & Sp. 1:56. 1815.
Piper latum H.B.K. loc. cit. 57. 1815.
Enckea smilacifolia Kunth, in Linnaea 13:605. 1839.
Enckea lata Kunth, loc. cit. 606. 1839.
Enckea reticulata Miq. Syst. Pip. 365. 1843.
Macropiper latum Presl, Epim. Bot. 223. 1849.
Piper Duchassaingii C.DC. in DC. Prodr. 16[1]:251. 1869.

A glabrous shrub or small tree up to 4–6 m. tall; branches slender, nodose; leaves elliptic, elliptic-ovate, or broadly ovate, 8–15 cm. wide × 15–25 cm. long or occasionally up to 25 cm. wide × 30 cm. long, apex acuminate, base essentially equilateral, more or less acute, truncated, or in large leaves shallowly cordate, palmately 5- to 7-nerved, or larger leaves 9-nerved, the nerves prominent beneath, reticulate-veiny with rather prominent cross-connecting nervules, drying firm and chartaceous; petiole 1–2 cm. long, glabrate or very obscurely puberulent-papillate, grooved above, vaginate near the base; spikes 5–6 mm. thick and up to 10 or 12 or occasionally 15 cm. long when mature; peduncle slender, 1–2 cm. long; rachis with membranous, fimbriated ridges; bracts peltately dilated upward, pedicel and margin bearded; stamens 4; fruit obovoid, somewhat 4-sided, papillate, with an apical, smooth, disc-like area, stigmas 3 or 4, rounded.

West Indies and on the mainland from Central America through northern South America.

BOCAS DEL TORO: Lower Changuinola River, *Stork 50.* CHIRIQUÍ: Progreso, *Cooper & Slater 185.* CANAL ZONE: along Caño Quebrado, *Pittier 6986;* around Gamboa, alt. 40–80 m., *Pittier 3778;* between Gorgona and Gatún, alt. 10–50 m., *Pittier 2279;* near Gatún, *Standley 27201;* Mamei Hill, alt. 20–90 m., *Pittier 3811;* near Summit, *Standley 25728;* Cerro Gordo, near Culebra, *Standley 26008;* Río Pedro Miquel, near East Paraíso, *Standley 29969;* vicinity of Fort Sherman, *Standley 30959;* Barro Colorado Island, *Standley 31267; Miller 2075;* Matachin, *Kuntze 1918;* Obispo, *Standley 31726;* vicinity of Gatuncillo, *Piper 5603, 5620;* Río Agua Salud, near Frijoles, *Piper 5859, 5860;* Empire, *Miller 1867;* Madden Dam Road, *Miller 1800;* along Río Chagres between Gamboa and Alahuela, alt. 30–60 m., *Allen 956.* COLÓN: between France Field and Cativa1, *Standley 30338;* along Río Fató, alt. 10–100 m., *Pittier 3872, 3882;* Fató, *Pittier 3842.* PANAMÁ: Río Tapia, *Standley 26160, 28035, 28241;* near Tapia River, Juan Díaz region, *Maxon & Harvey 6650, 6708;* Juan Díaz, *Standley 30548;* Río Tecumen, *Standley 29363.* DARIÉN: along Sambú River, *Pittier 5570.*

The large, glabrous, rather veiny leaves, comparatively short spikes, and especially the prominent glabrous disc at the top of the papillate fruit, characterize this species. There is a wide variation in the size of the leaves.

20. PIPER MARGINATUM Jacq. Icon. Pl. Rar. 2:2, *pl. 215.* 1786.

Piper decumanum Aubl. Pl. Guian. Fr. 1:21. 1775, not L. 1760, nor Miller 1763.
Piper caudatum Vahl, Eclog. Am. 1:3. 1796.
Piper alare Ham. Prodr. Pl. Ind. Occ. 3. 1825.
Schilleria caudata Kunth, in Linnaea 13:716. 1839.
Schilleria marginata Kunth, loc. cit. 718. 1839.
Artanthe caudata Miq. Syst. Pip. 380. 1843.
Artanthe marginata Miq. loc. cit. 381. 1843.
Artanthe alaris Miq. loc. cit. 406. 1843.

Piper regressum Anders. in Miq. loc. cit. 380. 1843, as synonym.
Piper san-joseanum C.DC. in Linnaea 37:351. 1872.
Piper san-joseanum var. *chiriquinum* Trel. in Ann. Mo. Bot. Gard. 25:826. 1938.
Piper san-joseanum var. *kobense* Trel. loc. cit. 27:297. 1940.
Piper san-joseanum var. *panamanum* Trel. loc. cit. 1940.
Piper san-joseanum var. *tabogense* Trel. loc. cit. 1940.

Fig. 4. *P. marginatum*

A shrub or small tree with moderate to rather short internodes; branches slender, glabrous and blackish when dry; leaves round-ovate, 8–15 cm. wide × 10–20 cm. long, or rarely some leaves somewhat larger, apex acuminate to long-attenuate-acuminate, base openly cordate or occasionally subtruncate, glabrous on both sides except for slight ciliation and submarginal silkiness, palmately 9- to 11-nerved, nerves entirely free, or the innermost pair of laterals slightly coalescing with the midrib at the base, cross-connecting and anastomosing nervules rather prominent, the leaf margins confluent across the top of the petiole, drying membranous, translucent, pellucid-dotted; petiole up to 4 cm. long or on larger leaves somewhat longer, vaginate-winged to near the blade; spikes 2–4 mm. thick when mature and up to 10–13 cm. or occasionally 20 cm. long; peduncle about 10 mm. long; bracts transversely triangular-peltate, marginally fringed; fruit smooth, obpyramidal, angular; stigmas 3, linear, sessile.

West Indies, on the mainland of Central America, and southward to Brazil and Ecuador.

Panama: without indication of locality, *Née 300, 387.* province (?): Santa Rita Trail, *Cowell 117, 122.* chiriquí: between Río Tabasara and Río Tinta, *Woodson, Seibert & Allen 416.* veraguas: Isla de Uva, Contreras group, *Pittier 5112.* coclé: El Valle, *Miller 1812.* canal zone: Monkey Hill above Colón, *Lehmann XLVI;* New Limón, *Stevens 1015;* Culebra, *Stevens 927;* Fort Kobe road, *Woodson, Allen & Seibert 1423;* western slope of Ancón Hill, vicinity of Balboa, alt. 20–75 m., *Seibert 388;* Ancón Hill, *Killip 3041, 12087; Standley 26326;* Balboa, *Standley 25600;* between Frijoles and Monte Lirio, alt. 30 m., *Killip 12116;* Frijoles, *Standley 27627;* Empire, *Miller 1862;* Juan Mina, *Piper 5696, 5698;* near old Fort Lorenzo, mouth of Río Chagres, *Piper 5898, 5917, 5962;* Culebra, alt. 50–150 m., *Pittier 2146;* Cerro Gordo, near Culebra, alt. 50–290 m., *Pittier 3737; Standley 25964;* Corozal, *Stevens 118;* Agua Clara Reservoir, *Stevens 546;* near Summit, *Standley 25751, 26938;* near Gatún, *Standley 27247, 27288;* Gamboa, *Standley 28334, 28536;* near Fort Randolph, *Standley 28655;* vicinity of Fort Sherman, *Standley 30042; Stevens 267;* Darién Station, *Standley 31557;* Barro Colorado Island, *Standley 40832; Kenoyer 599.* colón: between Fató and Playa de Damas, *Pittier 3934;* vicinity of Santa Isabel, *Pittier 4176.* panamá: Gorgona Beach, *Woodson, Allen & Seibert 1690;* Taboga

Island, alt. 0–186 m., *Woodson, Allen & Seibert 1531; Killip 3165, 3195; Miller 1848; Pittier 3553; Standley 27044, 27057, 27847;* Camino de la Granja, *Bro. Heriberto 166;* Bella Vista, *Killip 12012; Standley 25332;* Madden Lake, *Miller 2077;* near Punta Paitilla, *Standley 26274;* near big swamp, east of Río Tecumen, *Standley 26599;* along Corozal road, near Panamá, *Standley 26834;* Río Tapia, *Standley 28207;* between Fort Clayton and Corozal, *Standley 29214;* Río Tecumen, *Standley 29482;* Juan Díaz, *Standley 30521;* between Las Sabanas and Matías Hernández, *Standley 31835.* HERRERA: Pesé, alt. 50 m., *Allen 801.* DARIÉN: around Garachiné, *Pittier 5512.*

KEY TO THE VARIETIES OF *P. MARGINATUM*

a. Sinus wide, open, lobes more or less divergent.
  b. Leaves not pilose above, the nerves glabrous or puberulent.
    c. Nerves scarcely puberulent ..... 20. P. MARGINATUM
    cc. Nerves puberulent, at least above ..... 20a. var. ANISATUM
  bb. Leaves appressed-pilose above, at least toward the apex; nerves beneath pubescent ..... 20b. var. CATALPAEFOLIUM

aa. Sinus closed or nearly so, lobes approximated or overlapping ..... 20c. var. CLAUSUM

20a. PIPER MARGINATUM var. ANISATUM (H.B.K.) C.DC. in Urb. Symb. Ant. 3:172. 1902.

Piper anisatum H.B.K. Nov. Gen. & Sp. 1:58. 1815.
Piper san-joseanum var. *remediosense* Trel. in Ann. Mo. Bot. Gard. 27:297. 1940.

The nerves puberulent or hirtellous, at least on the upper surface.

Occurs with the species.

CHIRIQUÍ: Río Chiriquí to Remedios, alt. 15–50 m., *Woodson, Allen & Seibert 1191.* PANAMÁ: Perlas Archipelago, San José Island, *Johnston 319, 472;* Saboga Island, *Miller 1953;* along Chararé River, near Chepo, alt. 50–100 m., *Pittier 4708.* DARIÉN: trail between Pinogana and Yavisa, alt. 15 m., *Allen 260.*

20b. PIPER MARGINATUM var. CATALPAEFOLIUM (H.B.K.) C.DC. in DC. Prodr. 16[1]:246. 1869.

Piper catalpaefolium H.B.K. Nov. Gen. & Sp. 1:58. 1815.
Schilleria catalpaefolia Kunth, in Linnaea 13:718. 1839.
Artanthe catalpaefolia Miq. Versl. en Medel. Kon. Nederl. Inst. 1842:197. 1843.
Piper pseudomarginatum C.DC. in Bull. Herb. Boiss. 6:492. 1898.

Leaves appressed-pilose above, at least toward the apex, and pubescent along the nerves beneath.

Occurs with the species.

CANAL ZONE: Corozal, *Stevens 63.* PANAMÁ: Perlas Archipelago, Trapeche Island, *Miller 1907.* DARIÉN: vicinity of Boca de Cupe, alt. 40 m., *Allen 869.*

20c. PIPER MARGINATUM var. **clausum** Yuncker, var. nov.

Foliis suborbicularibus, basi profunde cordatis, sinu angustato, lobis approximatis vel invicem obtegentibus.

Leaves suborbicular, base deeply cordate with narrow sinus, the lobes approximated or overlapping.

Central Panama.

CANAL ZONE: Empire, March 5, 1937, *Miller 1861* (U. S. Nat. Herb., TYPE); vicinity of Salamanca Hydrographic Station, Río Pequení, alt. 80 m., July 28-29, 1938, *Woodson, Allen & Seibert 1608*—this specimen shows somewhat more open sinuses than does the type.

21. Piper **aristolochiaefolium** (Trel.) Yuncker, comb. nov.

Piper san-joseanum var. *aristolochiaefolium* Trel. in Contr. U. S. Nat. Herb. 26:22. 1927.

A shrub, 1.5–2 m. tall, twigs somewhat zig-zag, granular-papillate, moderately slender; leaves bullate and dark green when growing, rather narrowly ovate, apex long-acuminate, base deeply cordate, sinus open, obtuse, with parallel margins, 8–9 cm. wide × 15 cm. long, palmately 5-nerved, the innermost laterals not continuing to the apex, the midrib strongly branched upward, the nerves and cross-connecting-anastomosing nervules prominent beneath, the innermost pair of laterals entirely free from the midrib, with scattered, soft, white hairs above, paler and with the nerves granulate-papillate or subhirtellous beneath, ciliate, the hairs restricted to a single marginal row, pale-yellow-glandular-dotted beneath, drying thin, translucent; petiole 3–4 cm. long, vaginate to about the middle, scarcely winged, granulate-subhirtellous. No inflorescence present.

Known only from the type locality.

CANAL ZONE: wet forest, hills north of Frijoles, "scarce," Dec. 19, 1923, *Standley 27524* (U. S. Nat. Herb., TYPE).

The specimen on which this species is based is sterile but the vegetative characters are believed to be sufficiently different from *P. marginatum* to warrant specific rank. It differs from that species chiefly because of the 5-nerved leaves, the midrib strongly branched upward, the lateral nerves not continuing to the apex, the ciliation restricted to a single row of marginal hairs, and the shape of the basal sinus.

22. Piper humorigaudens Trel. in Ann. Mo. Bot. Gard. 27:293. 1940.

A branching, nodose, glabrous shrub, 2 m. tall; upper internodes short and slender, finely ribbed; leaves lanceolate, apex rather gradually blunt-acuminate, base inequilaterally narrowed downward, one side about 2 mm. shorter at the petiole, the shorter side acute, the longer side rounded, subacute, 2.5–3 cm. wide × 8–11 cm. long, 3-nerved, the nerves unevenly coalescing within the lowermost 5 mm., salient beneath, cross-connecting and anastomosing nervules very slender, drying rather firm, subtranslucent; petiole scarcely 5 plus 2 mm. long, vaginate near the base; spikes 3 mm. thick × 4–5 cm. long; peduncle 1–1.5 cm. long; rachis ridges fimbriate; bracts small, subcucullate, marginally short-fringed; fruit somewhat granular, depressed-subglobose, laterally compressed; stigmas sessile.

Known only from the following locality.

COCLÉ: wet north rim, El Valle, alt. 80–100 m., May 21, 1939, *Allen 1833*.

23. Piper conversum Trel. in Ann. Mo. Bot. Gard. 27:290. 1940.

Subarborescent, 2 m. tall; young branches nodose, very slender, internodes short, finely striate, obscurely and minutely hirtellous glabrescent; leaves lance-elliptic, apex caudately acuminate, base about 2 mm. shorter on one side, acute, 3–4.5 cm. wide × 10–12 cm. long, palmately 5-nerved with the outermost pair of nerves delicate and loop-connected with cross-connecting nerves upward, the innermost

pair of lateral nerves slightly coalescent with the midrib at the base, prominent beneath, drying thin, translucent; petiole about 3 mm. plus 2 mm. long, obscurely hirtellous, vaginate toward the base, the margin of the vagina ciliate; spikes as yet young, 2 mm. wide × 2.5 cm. long; peduncle 5 mm. long, glabrous; bracts inflexed-subpeltate, ciliate; ovary ovoid, stigmas apical.

Known only from the following collection.

CHIRIQUÍ: Llanos del Volcán, alt. about 1300 m., *Allen 1550.*

This species closely resembles *P. humorigaudens* but differs because of the shape of the 5-nerved, more attenuately acuminate leaves, subhirtellous twigs and petioles, and ciliate margins of the petiole vaginal groove.

24. PIPER PINOGANENSE Trel. in Contr. U. S. Nat. Herb. 26:22. 1927.

Piper tabasaranum Trel. in Ann. Mo. Bot. Gard. 25:827. 1938.
Piper salamancanum Trel. loc. cit. 27:296. 1940.

A shrub or small tree, 1.5–4 m. tall, nodose; internodes slender, rather short, minutely and transiently puberulent, finely ribbed; leaves elliptic, apex caudately blunt-acuminate, base rounded but subacute at the petiole, or narrowed and acute, 3–5.5 cm. wide × 8–12 cm. long, palmately 5-nerved, the nerves salient on both sides, the innermost pair of laterals coalescing with the midrib within the lowermost 5 mm., with numerous, fine, cross-connecting and anastomosing nervules, drying light green, firm, chartaceous, glossy, translucent; petiole scarcely 5 mm. long, granular-puberulent, channelled above, drying wrinkled, vaginate toward the base; spikes 3–4.5 cm. long, loosely flowered; peduncle scarcely 1 cm. long, obscurely puberulent; bracts very small, concave, glabrous; fruit ovoid, smooth or papillate; stigmas 3 or 4, sessile.

Panama.

CHIRIQUÍ: banks of lower Río Tabasará, *Woodson, Allen & Seibert 440.* CANAL ZONE: vicinity of Salamanca Hydrographic Station, Río Pequení, alt. 80 m., *Woodson, Allen & Seibert 1590.* DARIÉN: around Pinogana, *Pittier 6656.*

25. PIPER MEDIUM Jacq. Icon. Pl. Rar. 1:2. 1781.

Piper plantagineum Lam. Illustr. Encyc. Meth. 1:80. 1791.
Piper saururoides Ham. Prodr. Pl. Ind. Occ. 3. 1825.
Piper reticulatum Vell. Fl. Flum. 1: *pl. 61.* 1827, not L. 1753.
Piper syringaefolium Balbis ex Kunth, in Linnaea 13:599. 1839.
Piper orthostachyum Kunth, loc. cit. 602. 1839.
Enckea plantaginea Kunth, loc. cit. 599. 1839.
Enckea orthostachya Kunth, loc. cit. 601. 1839.
Enckea Sieberi Miq. Syst. Pip. 358. 1843.
Piper victorianum C.DC. in Jour. Bot. 4:218. 1866.
Piper tigerianum C.DC. loc. cit. 300. 1866.
Piper Sieberi C.DC. in DC. Prodr. 16^1:248. 1869.

A shrub; stems and branches glabrous or slightly puberulent when young; leaves lance- to round-elliptic or subrhombically obovate, 3.5–6 cm. wide × 8–11 cm. long, or rarely occasional leaves up to 10 × 14 cm., apex acuminate, base sometimes suboblique, acute or somewhat rounded, more or less subauriculate at

the very base, or lowermost somewhat cordate, glabrous or puberulent along the nerves beneath, palmately 5- to 7-nerved, reticulate-nervulose, drying membranous and minutely pellucid-dotted; petiole 5–10 mm. long, vaginate near the base, puberulent; spikes 4–5 mm. thick × 6–7 cm. long; peduncle 10–15 mm. long, puberulent or glabrous; rachis puberulent; bracts obovate-concave, somewhat papillate-pilose; fruit ovoid, minutely papillate or glabrous; stigmas 3 or 4, rounded, sessile.

West Indies, Central and South America.

CANAL ZONE: forest along banks of Quebrada Fea, Q. Pura and Cañon of Río Chagres, alt. 70–100 m., *Dodge & Hunter 17404*. CHIRIQUÍ: Cerro Galera Chorcha, vicinity of Gualaca, alt. 300 m., *Allen 5060*.

This species closely resembles *P. pinoganense* but differs primarily because of its more membranous leaves and hairy rachis and floral bracts.

III. KEY TO SPECIES WITH LEAVES MOSTLY 20 CM. OR MORE LONG AND MORE OR LESS LOBED AT THE BASE

(The base may be only slightly lobed but none are rounded or acute; the petiole mostly vaginate-winged to the middle or above.)

a. Leaves rugose or bullate.
  b. Leaves scabrid..... 41. P. PERACUMINATUM
  bb. Leaves not scabrid.
    c. Leaves loosely long-villous; peduncle 1–2 cm. long..... 26. P. PARTITICUSPE
    cc. Leaves hirtellous to pubescent; peduncle 1–2.5 cm. or more long.... 27. P. COOPERI
aa. Leaves scarcely rugose or bullate.
  b. Leaves and stems glabrous..... 28. P. HASTULARUM
  bb. Leaves and/or stems pubescent.
    c. Leaves scabrous..... 41. P. PERACUMINATUM
    cc. Leaves not scabrous.
      d. Leaf margin densely ciliolate, drying thin; spikes scarcely 5 mm. thick, yellow when dry..... 29. P. AURITUM
      dd. Leaf margin glabrous or essentially so.
        e. Young twigs, nodes and/or petioles and midrib beneath more or less fleshy-warty..... 30. P. IMPERIALE
        ee. Not fleshy-warty.
          f. Stems matted brown-hairy, leaves 5- to 7-nerved.
            g. Leaves acute, basal sinus wide, essentially glabrous above.... 31. P. TARDENS
            gg. Leaves acuminate; basal sinus narrow, nerves pubescent above..... 32. P. CAMPANUM
          ff. Stems glabrous; leaves mostly 7- to 9-nerved.
            g. Leaves glabrous above; petiole vaginate below the middle; bracts glabrate..... 33. P. CARRILLOANUM
            gg. Leaves more or less hairy above; petiole vaginate to the blade; bracts fringed..... 34. P. PITTIERI

26. PIPER PARTITICUSPE Trel. in Ann. Mo. Bot. Gard. 27:294. 1940.

Suffruticose, 3 m. tall; internodes comparatively slender and elongate, for a time crisp-villous; leaves round-ovate, apex falcately acuminate, base inequilaterally cordate with one side surpassing the petiole, sinus open, 15–28 cm. wide × 20–35 cm. long, pinnately nerved from the lower half, the nerves 6–8 on each side, with prominent cross-connecting and anastomosing nervules, venose-bullulate with 2–4

points to each cusp, the cusp points and the midrib near the base above long-villous, the nerves beneath loosely long-villous, drying firm, translucent; petiole 3–4 cm. long, densely villous; spikes 5 mm. thick × 15 cm. long; peduncle 1–2 cm. long, loosely villous; bracts triangular-subpeltate, slightly ciliate; fruit small, subtrigonous, glabrous; stigmas small, sessile.

Known only from the one locality.

COCLÉ: vicinity of El Valle, alt. 600–1000 m., *Allen 1195*.

The villous, round-ovate leaves with multipointed, villous, bullulate elevations characterize this species.

27. PIPER **Cooperi** Yuncker, sp. nov.

Frutex vel arbuscula, 5 m. altus; internodiis floriferis sat crassiusculis elongatisque conferte crispe-pubescentibus; foliis elliptico-subovatis rugosis, apice breviter subacuminatis, basi oblique cordatis, latere longiore petiolum excedente, infra medium pinnatim venosis, venis utrinque 6–7, laminae facie supra hirtella infra pubescente (ad venas quam maxime); petiolo 4–5 cm. longo, ad medium vel ultra vaginato-alato, conferte crispe pubescente; spicis immaturis 3 mm. crassis, 6 cm. longis; pedunculo 2.5–4 cm. longo, pubescente; bracteis rotundato-subpeltatis, atro-pubescentibus.

A shrub or small tree, 5 m. tall; stem 8 cm. thick, with clustered basal shoots; flowering internodes moderately stout and elongated, matted-crisp-pubescent; leaves elliptic-subovate, apex shortly subacuminate, base obliquely cordate, the longer lobe surpassing the petiole, 15–20 cm. wide × 16–30 cm. long, pinnately nerved from the lower half, the nerves 6 or 7 on each side, with cross-connecting and anastomosing nervules, hirtellous above, at least along the nerves, pubescent beneath, the nerves densely so, bullate, drying dark, firm, opaque; petiole 4–5 cm. long, vaginate-winged to the middle or above, densely crisp-pubescent; spikes as yet young, 3 mm. thick × 6 cm. long; peduncle 2.5–4 cm. long, pubescent; bracts round-subpeltate, dingy-hairy.

Known only from the type locality.

BOCAS DEL TORO: vicinity of Almirante, Daytonia Farm, Jan.-Mar. 1928, *G. Proctor Cooper 374* (U. S. Nat. Herb., TYPE).

This species differs from *P. partiticuspe,* which it resembles somewhat, because of the character of the pubescence, longer peduncles, pubescent bracts, etc.

28. PIPER **hastularum** Yuncker, sp. nov.

Frutex primo intuitu glaber, ligno molli, 1–3 m. altus; internodiis floriferis elongatis crassiusculisque; foliis lanceolato-ovatis vel late lanceolatis, 6–11 cm. latis, 22–29 cm. longis, apice sensim acutis acuminatisve, basi oblique inaequilateralibus, ad petiolum utrinque obtusis vel latere altero obtuso acutove ad petiolum 3–10 mm. breviore, caetero rotundato-obtuso subcordatove, a tertio supero pinnatim venosis, venis utrinque 4–5, venulisque submarginalibus gracilibus puberulis, subtus prominentibus trabibus anastomosantibus manifestis, arctius revolutis,

Fig. 5. *Piper hastularum*

opacis; petiolo 20–25 cum 3–10 mm. longo, ad laminam vaginato-alato; spicis 3–4 mm. crassis, 13 cm. longis apiculatis; pedunculo 10-20 mm. longo, gracili; bracteis triangulari-sublunatis margine tantum papillatis; drupa laevi, subglobosa, truncata; stigmatibus 3, linearibus, sessilibus.

An essentially glabrous, soft-wooded shrub, 1–3 m. tall; flowering internodes moderately slender to stoutish; leaves lance-ovate or broadly lanceolate, apex gradually sharp-acute to acuminate, base obliquely inequilateral, one side 3–10 mm. shorter at the petiole, both sides obtuse at the petiole or the shorter side subacute, the longer sometimes subcordate, 6–11 cm. wide × 22–29 cm. long, pinnately nerved below the upper third, the nerves 4–5 on each side, somewhat raised beneath, with rather strong cross-connecting nervules, the submarginal nervule more or less papillate or puberulent, drying chartaceous-subcoriaceous, opaque, somewhat glossy, narrowly revolute, glandular-dotted and sometimes microscopically black-mottled beneath; petiole 20–25 plus 3–10 mm. long, strongly vaginate-winged to the blade; spikes 3–4 mm. thick × 13 cm. long; peduncle slender, about 1–2 cm. long; bracts narrowly triangular- or lunate-subpeltate, smooth or papillate, the pedicel broad, concave, glabrous or ciliate; fruit truncate-subglobose, glabrous; stigmas sessile.

Western Colombia and Panama.

Colombia: chocó: Bahía Solano, dense forest along Quebrada Jellita, alt. 50–100 m., Feb. 22, 1939, *Killip & Garcia 33568* (U. S. Nat. Herb., type).

Panamá: bocas del toro: Old Bank Island, *von Wedel 1934.* coclé: El Valle de Antón, along Río Indio Trail, alt. 500–700 m., *Hunter & Allen 316.* darién: Chepigana District, Caña-Cuasi Trail (Camp 2), alt. 1200 m., March 10, 1940, *Terry & Terry 1461.*

The lanceolate leaves and submarginal puberulent nervules distinguish this species.

29. Piper auritum H.B.K. Nov. Gen. & Sp. 1:54. 1815.

Schilleria aurita Kunth, in Linnaea 13:713. 1839.
Artanthe aurita Miq. Syst. Pip. 400. 1844.
Artanthe Seemanniana Miq. in Seem. Bot. Voy. Herald, 199, *pl. 39.* 1854, not *Piper Seemannianum* C.DC.
Piper auritum var. *amplifolium* C.DC. in DC. Prod. 16[1]:321. 1869.
Piper auritum var. *Seemannianum* (Miq.) Trel. in Contr. U. S. Nat. Herb. 26:40. 1927.
Piper heraldi Trel. in Ann. Mo. Bot. Gard. 27:292. 1940.
Piper heraldi var. *amplius* Trel. loc. cit. 1940.

Piper heraldi var. *cocleanum* Trel. loc. cit. 1940.
Piper Alstoni Trel. loc. cit. 286. 1940.

A small, soft-wooded, commonly more or less aromatic tree, 3–6 m. tall, often occurring in clumps; flowering internodes moderately slender and long, striate, often drying black, glabrate or sometimes slightly pubescent; leaves ovate, oblong- or elliptic-ovate, 12–20 cm. wide × 20–30 cm. long, or occasionally up to 25 × 40 cm. or more, apex acute or short-acuminate, base deeply cordate with one side 1–2 cm. longer at the petiole and with the lower lobe longer, sinus rounded to the petiole, the midrib with 3 or 4 upcurved branches from below the upper third and 3 or 4 branches from the base, rather thinly short-hairy above at least along the nerves, more densely so beneath, densely white-ciliolate throughout, drying thin, translucent; petiole 4–9 plus 1–2 cm. long, more or less pubescent or glabrate, vaginate-winged to the blade; spikes creamy or light-yellow when dry, 3–5 mm. thick × 10–25 cm. long; peduncle slender, 2–8 cm. long, glabrate, often black when dry; bracts round- or triangular-subpeltate, marginally fringed; fruit small, glabrate, obpyramidal-trigonous; stigmas 3, sessile.

West Indies and on the mainland from Mexico through Central America and northern South America.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 403;* Laguna de Chiriquí, *Hart 126;* vicinity of Nievecita, alt. 0–50 m., *Woodson, Allen & Seibert 1813;* vicinity of Chiriquí Lagoon, *von Wedel 1194.* CHIRIQUÍ: Finca Lérida to Boquete, alt. 1300–1700 m., *Woodson, Allen & Seibert 1095;* Cerro de la Plata, near San Felix, alt. 120–150 m., *Pittier 5159;* vicinity of David, alt. 30–80 m., *Pittier 2829.* COCLÉ: Penonomé, *Williams 434;* north rim of El Valle, *Alston & Allen 1842;* vicinity of El Valle, alt. 600–1000 m., *Allen 1192.* CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 27; Bangham 590;* Monkey Hill, *Lehmann 1004; Cowell 22;* between Chagres Batteries and Fort San Lorenzo, Fort Sherman Military Reservation, *Maxon & Valentine 6983;* Río Agua Salud, near Frijoles, *Piper 5844;* between Gorgona and Gatún, alt. 10–50 m., *Pittier 2263;* Gatún, *Standley 27244; Stevens 833; Riley 108;* Fort Sherman, *Standley 30934; Stevens 263;* headwaters of the Río Chinilla, above Nuevo Limón, *Maxon 6898;* forests of northerly arm of Quebrada Salamanca as far as falls, alt. 70 m., *Steyermark & Allen 17140.* COLÓN: "Aspinwall," *Hayes 835;* around Porto Bello, alt. 5–100 m., *Pittier 2441;* beach between Fató and Playa de Damas, *Pittier 3933;* along Río Fató, alt. 10–100 m., *Pittier 3909;* vicinity of Santa Isabel, *Pittier 4177;* Puerto Obaldía, San Blas coast, alt. 0–50 m., *Pittier 4380.* PANAMÁ: Manzanillo Island, *Hayes 40, 706;* Chararé River, near Chepo, alt. 100–200 m., *Pittier 4709;* vicinity of Arenoso, lower Río Trinidad, alt. 26–50 m., *Seibert 623.* DARIÉN: Boca de Cupe, *Williams 785;* headwaters Río Chico, alt. 150–225 m., *Allen 4603.*

The thin, deeply and inequilaterally cordate leaves more or less pubescent on both sides and densely ciliolate, long, blackening peduncles, and comparatively small, yellowish spikes distinguish this species.

30. PIPER IMPERIALE (Miq.) C.DC. in DC. Prodr. 16^1:339. 1869.

Artanthe imperialis Miq. in Seem. Bot. Voy. Herald, 198. 1854.
Piper portobellense C.DC. Smiths. Misc. Coll. 71^6:6. 1920.
Piper affectans Trel. in Ann. Mo. Bot. Gard. 27:287. 1940.
Piper frijolesanum Trel. var. *grandifolium* Trel. loc. cit. 291. 1940.
Piper gigas Trel. loc. cit. 292. 1940.

A shrub or small tree, commonly 2–5 m. tall; flowering internodes rather elongate and stoutish, commonly somewhat fleshy-warty especially near the nodes,

pubescent or glabrescent; leaves broadly ovate, apex acute or short-acuminate, base somewhat obliquely cordulate with a rather narrow sinus, both sides essentially equal at the petiole or one side a few mm. shorter, up to 29 cm. wide × 50 cm. long but usually somewhat smaller, pinnately nerved below the upper third or fourth, the nerves 7–8 on each side, the lowermost 3 or 4 approximated near the base, with cross-connecting and anastomosing nervules, submarginally loop-connected, glabrous above, pubescent beneath, at least the nerves puberulent, the midrib beneath with warty excrescences at least near the base, drying firm, brown, opaque; petiole 6–8 or 12 cm. long, puberulent, vaginate-winged nearly to the blade, with warty-excrescences; spikes 8–10 mm. thick × 30–50 cm. or more long; peduncle 4–6 cm. or more long, sparsely hairy glabrescent; bracts rounded- or triangular-subpeltate, inflexed, yellow-puberulent or glabrate; fruit rather large, obovoid, glabrous, stigmas linear, on a short, stout, deciduous style.

Panama.

CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., *Woodson, Allen & Seibert 846, 865;* Boquete District, Bajo Chorro, alt. 1800 m., *Davidson 374.* COCLÉ: vicinity of El Valle, alt. 600–1000 m., *Allen 1193.* CANAL ZONE: between Frijoles and Monte Lirio, alt. 30 m., *Killip 12155;* hills north of Frijoles, *Standley 27441;* Barro Colorado Island, *Standley 31273, 41115.* COLÓN: forests around Porto Bello, alt. 5–200 m., *Maxon 5795.* PANAMÁ: Taboga Island, *Née 350.* DARIÉN: Chepigana Distr., Caña-Cuasi Trail, alt. 600 m., *Terry & Terry 1500.*

The types of *P. affectans* and *P. frijolesanum* var. *grandifolium* are less warty and the stems are more glabrous than with the other specimens cited, while the young growth of the type of *P. gigas* is somewhat more densely pubescent. The type specimens of both *P. affectans* and *P. gigas* are stated as being trees and with a trunk 30 cm. in diameter. No other differences have been noted in the herbarium specimens, and it is believed that they all represent variations of the same species. So far as discovered, *P. frijolesanum* is a *nomen nudum* as used for var. *grandifolium.*

31. PIPER TARDENS Trel. in Ann. Mo. Bot. Gard. 27:298. 1940.

A shrub or small tree, 1–5 m. tall; flowering internodes rather slender and elongated, densely brown-tomentose-pubescent; leaves pentagonally ovate, apex acute, base inequilaterally oblique, rather shallowly and openly cordate, 10–16 cm. wide × 17–28 cm. long, pinnately nerved from the lower half, the nerves 5–6 on each side, salient beneath, with rather prominent cross-connecting and anastomosing nervules, glabrous above or the midrib sparsely pubescent near the base, hirsute beneath, the nerves densely so, drying coriaceous, opaque; petiole 3–5 cm. long, vaginate-winged to the blade, densely tomentose-pubescent; spikes 5–8 mm. thick × 25 cm. long; peduncle 2.5–4 cm. long, densely hairy; bracts rounded- or triangular-subpeltate; pedicel brown-villous; fruit globose, stigmas sessile or on a short style (?).

Chiriquí, Panama.

CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., *Woodson, Allen & Seibert 848;* Boquete Distr., Bajo Chorro, alt. 1800 m., *Davidson 78, 373.*

The densely matted twigs, pentagonally-ovate leaves, glabrous above and hirsute beneath, are characteristic of this species. From the material at hand it has not been possible to determine with certainty regarding the presence of a style. Most of the fruit examined do not exhibit any but in a few there appeared to be a short, thick style. This condition, however, may have resulted from the manner in which the fruit dried and may not represent a true style.

32. PIPER **campanum** Yuncker, sp. nov.

Frutex 2 m. altus, internodiis superis gracilibus elongatis, conferte brunneo-pubescentibus; foliis lanceolato-ovatis, apice sat attenuatim acuminatis, basi cordato-auriculatis, latere altero 5 mm. breviore, sinu obliquo, a tertio supero deorsum pinnatim venosis, venis utrinque 6–7, utrinque ad venas pubescentibus, glanduloso-punctatis; petiolo 2.5–4.5 cm. cum 2–5 mm. longo, conferte brunneo-pubescente, ad laminam vaginato-alato; spicis immaturis, 1 mm. crassis, 5 cm. longis; pedunculo gracili, conferte pubescente.

A shrub, 2 m. tall; upper internodes slender and elongate, densely brown-matted-hairy; leaves lance-ovate, apex somewhat attenuately acuminate, base cordate-auriculate, one side up to 5 mm. shorter at the petiole, the sinus lateral, 11–12 cm. wide × 26 cm. long, or upper leaves smaller, pinnately nerved below the upper third, the nerves 6–7 on each side, branched upward to some extent, with cross-connecting and anastomosing nervules, the nerves pubescent on both sides or only toward the base on the upper surface, drying rather thin, subtranslucent, glandular-dotted; petiole 2.5–4.5 plus 2–5 mm. long, densely brown-hairy, vaginate-winged to the blade; spikes as yet very young, 1 mm. thick × 5 cm. long; peduncle slender, 1 cm. long, densely hairy; bracts subpeltate, bristly.

Known only from the type locality.

PANAMÁ: Cerro Campana, vicinity of Campana, alt. 1000 m., April 21, 1941, *Allen 2411* (U. S. Nat. Herb., TYPE).

This species resembles *P. tardens* to some extent but differs because of the more acuminate leaf apex, cordate-auriculate base, and more pubescent nerves above.

33. PIPER CARRILLOANUM C.DC. in Bull. Soc. Roy. Bot. Belg. 30^1:209. 1891.

Piper vallicolum C.DC. loc. cit. 222. 1891.
Piper paulownifolium C.DC. in Anal. Inst. Fis. Geogr. Costa Rica 9:173. 1898.
Piper tiliaefolium Cham. & Schlechtd. var. *paulownifolium* C.DC. in Candollea 1:154. 1923.
Piper Omega Trel. in Contr. U. S. Nat. Herb. 26:146. 1929.

A shrub, 2–4 m. tall, glabrous except the puberulous nerves on the lower surface; upper internodes moderately slender and elongated; leaves subequilaterally ovate, apex rather long-acuminate, base subtruncate to moderately deeply cordate with open sinus, the blade margin commonly meeting over the petiole, rather small and elongate, 6–8 cm. wide × 15 cm. long or becoming more rounded and as much as 25 × 35 cm., pinnately nerved to about the middle, 7–9 nerves on each side, the lowermost 3–5 from near the base, salient beneath, with prominent cross-connecting and anastomosing nervules, very finely nervulose by transmitted light,

drying light green, papery, translucent; petiole slender, 2–5 or even 10 cm. long, vaginate winged below the middle; spikes about 3 mm. thick × 15–25 cm. long; peduncle 1–2 cm. long; bracts small, triangular-subpeltate, glabrate; fruit small, obpyramidal-trigonous, gray-papillate, stigmas small, sessile.

Costa Rica and Panama.

CHIRIQUÍ: Cerro de la Plata, near San Felix, alt. 120–150 m., *Pittier 5158*; Paso de Quebrada Gata, between Hato Jobo and San Felix, *Pittier 5427*. CANAL ZONE: hills north of Frijoles, *Standley 27612*; hills west of the canal, near Gatún, *Standley 27226*; Mamei Hill, alt. 20–90 m., *Pittier 3812*; along Caño Quebrado, *Pittier 6666*; Barro Colorado Island, *Miller 2073*; *Maxon, Harvey & Valentine 6809*; *Standley 31282, 31293, 40870, 40064*; *Bailey & Bailey 30*; *Stevens 645*; Pearson Trail, alt. 100 m., *Wetmore & Abbe 123*; between Gorgona and Gatún, alt. 10–50 m., *Pittier 2261*. COLÓN: Fató (Nombre de Dios), *Pittier 3844*. DARIÉN: Boca de Pauarandó, on Sambú River, alt. 20 m., *Pittier 5687*; Chepigana Distr., Caña-Cuasi Trail, alt. 600 m., *Terry & Terry 1475*.

This species closely resembles *P. casimirianum* Hemsl. of Nicaragua from which it appears to differ because of the leaf shape and puberulence, as described. It is also quite similar to *P. zacuapanum* of Mexico and may, indeed, be the same. The great variation in the size of the leaves often on the same specimen, leaf shape, puberulent nerves beneath, etc. are distinguishing characteristics.

34. PIPER PITTIERI C.DC. in Bull. Soc. Bot. Belg. 29^2:69. 1890; 30^1:204. 1891.

A soft shrub, 1 m. or more tall; flowering internodes rather thick and elongated, glabrous, glandular-dotted; leaves broadly ovate, apex abruptly acute or short-acuminate, base truncately shallow-cordate, 14–16 cm. wide × 15–22 cm. long, pinnately nerved from below the upper third, the nerves about 8 on each side, gradually approximated downward, submarginally loop-connected, with rather prominent cross-connecting-anastomosing nervules, thinly pubescent above, the nerves beneath rather densely villous laterally, ciliate, strongly glandular-dotted on both sides, drying rather thin but firm, translucent; petiole about 6 cm. long, vaginate-winged to the blade, glabrous, glandular-dotted; spikes 5 mm. thick × 15 cm. long or in fruit up to 12 mm. thick × 18 cm. long; peduncle stout, 1.5–2.5 cm. long, puberulent glabrescent, glandular-dotted; bracts triangular-subpeltate, narrowly fringed; fruit angularly oblong, with pointed, substylose apex, stigmas 3.

Costa Rica and adjacent Panama.

BOCAS DEL TORO: Robalo Trail, northern slopes of Cerro Horqueta, alt. 1800–2100 m., *Allen 5012*.

The large, somewhat pubescent leaves, rather large spikes, and substylose fruits are distinctive characters of this species.

IV. KEY TO SPECIES PINNATELY NERVED FROM SOMEWHAT BELOW THE MIDDLE TO THE UPPER THIRD OF THE BLADE AND WITH THE LEAVES MOSTLY LESS THAN 20 CM. LONG; IF LONGER, THE BASE IS NOT LOBED.

a. Leaves scabrous.
  b. Twigs glabrous.
    c. Leaves glabrous on both sides, scabrous beneath, smooth above..... 35. P. DAVIDANUM
    cc. Leaves hairy beneath, at least along the nerves.
      d. Leaves mostly 3–4.5 cm. wide, strongly granular-dotted beneath.. 36. P. MINUTE-SCABIOSUM

dd. Leaves 5–6 cm. wide, scarcely granular-dotted beneath..... 52. P. STORKII
bb. Twigs more or less hairy, at least when young.
c. Spikes strongly and regularly curved; peduncle longer than the petiole..... 37. P. ADUNCUM
cc. Spikes not strongly or regularly curved.
d. Stem hairs stiff-hispid, comparatively short; leaves harshly scabrous; fruit papillate-puberulent at apex..... 38. P. HISPIDUM
dd. Stem hairs retrorse; leaves finely scabrous.
e. Plant scandent; leaf base obtuse or acutish..... 39. P. VITABUNDUM
ee. Plant shrubby; leaf base rounded, cordulate..... 78a. P. WEDELII var. RETROHIRSUTUM
ddd. Stem more softly pubescent or villous.
e. Hairs on the midrib beneath erect or at least not upcurved-strigose.
f. Hairs on midrib beneath mostly up to 1 mm. or more long.
g. Leaves mostly 18–20 cm. or more long.
h. Leaves 6–8 cm. wide, very slenderly acuminate, base obtuse or cordulate..... 40. P. PERSUBULATUM
hh. Leaves mostly 10 cm. or more wide, not slenderly acuminate, base rounded-cordate..... 41. P. PERACUMINATUM
gg. Leaves scarcely up to 15 cm. long.
h. Leaves broadly elliptic, less than two times longer than wide..... 73. P. CATIVALENSE
hh. Leaves 2–3 times longer than wide.
i. Leaves rhomboid-elliptic, strongly inequilateral; bracts glabrous..... 42. P. ERUBESCENTI-SPICUM
ii. Leaves lance-elliptic, elliptic, or elliptic-obovate.
j. Petioles scarcely 5 mm. long; stem hairs scarcely 1 mm. long; blades slightly scabrous..... 72. P. PSEUDO-GARAGARANUM
jj. Petioles up to 2 cm. long downward.
k. Blades mostly 5–8 cm. wide, scarcely scabrous above..... 43. P. CULEBRANUM
kk. Blades 3–4.5 cm. wide, harshly scabrous above.. 44. P. VIRIDICAULE
ff. Hairs on midrib mostly scarcely 0.5 mm. long, dense.
g. Leaves less than 5 cm. wide; veins above impressed in age.. 45. P. PERVELUTINUM
gg. Leaves 6–8 cm. wide; veins not impressed..... 46. P. VARIITRICHUM
ee. Hairs on the midrib beneath strongly upcurved and appressed or strigose.
f. Leaves less than 4 cm. wide..... 47. P. CHANGUINOLANUM
ff. Leaves mostly wider.
g. Blades moderately to densely hairy on the upper surface.
h. Peduncle scarcely 5 mm. long; blades villous above and harshly scabrous; bracts of young spikes not conspicuously bristly..... 48. P. VILLIRAMULUM
hh. Peduncle 5–10 mm. or more long; blades crisp-hirtellous or subhispid above, slightly scabrous; young spikes very short, conspicuously bristly from erect marginal hairs.
i. Leaves mostly narrowed downward, usually only the longer side rounded at the base..... 49. P. TABOGANUM
ii. Leaves rounded-cordulate on both sides..... 50. P. PSEUDO-CATIVALENSE
gg. Blades sparsely hairy or glabrous, hairy mostly only along the nerves above.
h. Young spikes not conspicuously bristly because of the erect bract hairs.
i. Bracts prominently densely yellow-fringed..... 70. P. LEPTOCLADUM
ii. Bracts very narrowly and sparsely fringed.
j. Nerves beneath spreading-hirsute..... 51. P. LUCIGAUDENS
jj. Nerves beneath obscurely strigose..... 52. P. STORKII
iii. Bracts glabrous, with a dorsal callus..... 78. P. WEDELII
hh. Young spikes about 1 cm. long, conspicuously bristly because of erect bract hairs..... 49. P. TABOGANUM

aa. Leaves not noticeably scabrous.
b. Spikes short, scarcely exceeding 2 cm. in length.
c. Stems and leaves glabrous.
d. Spikes less than 1 cm. long; bracts glabrous..... 53. P. Wagneri
dd. Spikes about 2–3 cm. long; bracts densely ciliate..... 54. P. Dunlapi
cc. Stems and/or leaves hairy.
d. Stems glabrous or sparsely pubescent; nerves beneath appressed-puberulent..... 55. P. palmasanum
dd. Stems rather densely hairy, at least when young..... 16. P. colon-insulae
bb. Spikes longer, mostly 3–5 cm. or more long (or unknown).
c. Stems and leaves essentially glabrous (nerves hirtellous or puberulous in *P. carrilloanum* and *P. aequale* var. *laurifolium*).
d. Peduncle 4–7 cm. long..... 56. P. reptabundum
dd. Peduncle scarcely 2 cm. long at most.
e. Leaves ovate.
f. Base mostly acute at the petiole; petiole 1–2.5 cm. long..... 57. P. chiriquinum
ff. Base obtuse to cordate.
g. Leaves 10–14 cm. long; petiole 5 mm. long..... 65. P. tecumense
gg. Leaves 15 cm. or more long; petiole 1–2 cm. or more long.
h. Nerves beneath puberulous; peduncle 1–2 cm. long. .. 33. P. carrilloanum
hh. Nerves beneath glabrous; peduncle 0.5–1 cm. long..... 93. P. grande
ee. Leaves elliptic, lance-elliptic, subobovate or obovate.
f. Leaves mostly 2.5–4.5 cm. wide (rarely wider); apex sharp- to strongly mucronate-acuminate.
g. Leaves scarcely more than 2–2½ times longer than wide.
h. Base acutely decurrent, apex strongly mucronate..... 58. P. tenuimucronatum
hh. Base rounded, obtuse..... 59. P. septuplinervium
gg. Leaves mostly 3–4 times longer than wide, or base not decurrent.
h. Bracts smooth; leaves not glandular.
i. Leaf base rounded, obtuse; nerves 4–5 on each side.... 59. P. septuplinervium
ii. Leaf base narrowed, acute to cuneate; nerves 3–4 on each side..... 60. P. subquinquenerve
hh. Bracts conspicuously yellow-fringed; leaves more or less glandular-dotted.
i. Leaves drying dull, yellow..... 61. P. infraluteum
ii. Leaves drying glossy, green..... 80b. P. hirtellipetiolum var. Harveyanum
ff. Leaves larger, mostly 5 cm. or more wide.
g. Leaves nerved from about the lower third, sharply abruptly acuminate..... 62. P. cricamolense
gg. Leaves nerved to about or above the middle.
h. Leaves mostly 4- to 5-nerved on each side of the midrib (or sometimes 6 in *P. aequale*).
i. Leaves obovate, revolute, apex mostly obtuse..... 10. P. macropunctatum
ii. Leaves oblong-elliptic-subobovate, apex abruptly blunt-acuminate..... 63. P. aequale
iii. Leaves elliptic, apex gradually acuminate.
j. Leaves, petioles, etc. strongly glandular-dotted . 64. P. sambuanum
jj. Leaves, etc. not glandular-dotted..... 65. P. tecumense
hh. Leaves 7-nerved on each side of the midrib, oblong-ovate, 10–13 cm. wide..... 66. P. crassispicatum
cc. Stems and/or leaves more or less hairy (minutely and obscurely so in *P. callibracteum*).
d. Leaves nerved from the lowermost ¼ or ⅓..... 67. P. bogotense
dd. Leaves nerved mostly to about the middle or above.
e. Leaf base with one side strongly auriculate and covering the petiole (auricle about 1 cm. or more long).
f. Pubescence strongly dimorphic; leaves 6 cm. or more wide.... 68. P. sperdinum
ff. Pubescence not dimorphic; leaves less than 5 cm. wide..... 69. P. perbrevicaule
ee. Leaf base may be cordulate but scarcely auriculate.
f. Leaves hairy on the upper surface, at least along the midrib above the very base.

g. Leaves 10 × 25 cm. or more ..... 85. P. COLONENSE
gg. Leaves mostly smaller.
h. Pubescence on the upper leaf surface restricted to the nerves.
i. Nerves beneath glabrous; spike 2–3 cm. long ..... 59a. P. SEPTUPLINERVIUM var. SUBPUBINERVIUM
ii. Nerves beneath obviously hairy ..... 70. P. LEPTOCLADUM
hh. Pubescence not so restricted.
i. Leaves 6–7 cm. wide, scarcely 3 times longer than wide; spikes straight.
j. Crisp-hirtellous or subhispid above; young spikes short, bristly ..... 49. P. TABOGANUM
jj. Sparsely long-villous above, glabrescent; young spikes not noticeably bristly.
k. Peduncle up to 6 cm. long; stem and leaf hairs strongly dimorphic ..... 71. P. DIMORPHOTRICHUM
kk. Peduncle much shorter; hairs not obviously dimorphic.
l. Apex gradually acuminate, blades 15–20 cm. long ..... 72. P. PSEUDO-GARAGARANUM
ll. Apex abruptly acuminate, blades 12–14 cm. long ..... 73. P. CATIVALENSE
ii. Leaves mostly narrower, 3–4 times or more longer than wide, rugescent, appressed-pubescent above; spikes commonly curved.
j. Nerves mostly 7–8 on each side; leaves mostly 3–5 cm. or more wide ..... 74. P. PSEUDO-LANCEAEFOLIUM
jj. Nerves mostly 4–5 on each side; leaves mostly 2–3.5 cm. wide ..... 75. P. LINEARIFOLIUM
ff. Leaves glabrous above.
g. Fruit and ovary papillate-pubescent.
h. Petioles scarcely 10 mm. long.
i. Spikes 2–3 mm. × 7–8 cm.; plant vine-like ..... 39. P. VITABUNDUM
ii. Spikes 3–5 mm. × 4–5 cm.; plant shrubby ..... 76. P. PANAMENSE
hh. Petioles up to 3 cm. long; spikes 8–10 cm. long ..... 77. P. CALLIBRACTEUM
gg. Fruit glabrous, or unknown.
h. Stems glabrous or essentially so.
i. Leaf nerves beneath thinly strigose; bracts glabrous .... 78. P. WEDELII
ii. Leaf nerves beneath obscurely puberulent; bracts fringed.
j. Leaves 7–10 cm. wide ..... 79. P. VERRUCULAE-PETIOLUM
jj. Leaves less than 6 cm. wide ..... 65. P. TECUMENSE
hh. Stems obviously pubescent, at least when young.
i. Leaf base narrowed, acute or obtusish, the sides nearly equal.
j. Nerves beneath glabrous; spikes about 4–5 cm. long ..... 80. P. HIRTELLIPETIOLUM
jj. Nerves beneath pubescent; spikes 5–6 cm. long .... 80a. P. HIRTELLIPETIOLUM var. TAPIANUM
ii. Leaf base with one or both sides rounded-obtuse, or the longer side mostly cordulate.
j. Bracts conspicuously fringed; spikes 3–4 mm. thick.
k. Lateral nerves loop-connected upward, not continuing toward the apex ..... 81. P. SUBCAUDATUM
kk. Lateral nerves not strongly loop-connected upward, continuing unbroken toward the apex ..... 43. P. CULEBRANUM
jj. Bracts essentially glabrous; spikes 7–8 mm. thick ... 82. P. GONOCARPUM

35. Piper davidanum C.DC. in Smiths. Misc. Coll. 71[6]:9. 1920.

A shrub, 2 m. tall, nodose; flowering internodes moderately slender, glabrous, granular, with subnodal lenticels; leaves elliptic, apex rather short-acuminate, base inequilateral, one side 4–5 mm. shorter and acute, the longer side rounded, 6–9 cm. wide × 16-19 cm. long, glabrous on both sides, finely scabrous and glandular-dotted beneath, smooth above, pinnately nerved below the upper third, the nerves rather prominent beneath, 5–6 on each side, with slender cross-connecting and anastomosing nervules, drying pale green, membranous, translucent; petiole 6 plus 4–5 mm. long, vaginate at the base, glabrous; spikes 3 mm. thick × 8–10 cm. long; peduncle 5–7 mm. long, glabrous; bracts triangular-lunate-subpeltate, sparsely papillate-fringed; fruit oblong-tetragonous, granulate-papillate at the top, stigmas sessile.

Known only from the following locality.

chiriquí: vicinity of David, along streamlet, alt. 30–80 m., *Pittier 2837*.

The glabrous stems and leaves, and scabrous lower leaf surface characterize this species.

36. Piper minute-scabiosum Trel. in Ann. Mo. Bot. Gard. 27:294. 1940.

Piper minute-scabiosum var. *arborescens* Trel. loc. cit. 1940.

A shrub or small tree, up to 3 m. tall, somewhat twiggy, nodose; flowering internodes slender, lepidote-granular, glabrous; leaves narrowly elliptic or lance-elliptic, apex caudately acuminate, base inequilateral, acute or obtuse, one side 1–3 mm. shorter, 2.5–4 cm. wide × 9–15 cm. long, pinnately nerved from the lower half, the nerves 4 or 5 on each side, with inconspicuous cross-connecting nervules, glabrous and smooth above, scabrous and the nerves strigose-hairy beneath, glandular-dotted on both sides, drying rather firm, translucent; petiole 5–8 plus 1–3 mm. long, granular, vaginate at the base; spikes 2–3 mm. thick × 8 cm. long, cuspidate; peduncle 1–1.5 cm. long, glabrous; bracts triangular-lunate-subpeltate, rather sparsely short-fringed; ovary compressed-ovoid, papillate about the apex; stigmas sessile.

Known only from the following locality.

coclé: north rim of El Valle de Antón, alt. 600–1000 m., *Allen 1639;* vicinity of El Valle, alt. 600–1000 m., *Allen 1185;* along Rio Indio Trail, alt. 500–700 m., *Hunter & Allen 333*.

The only difference which can be noted between the type of the variety and that of the species is the collectors' notations of the habit of growth. Because of the great variation in this character it is not believed to be valid in this case. The species was described as a shrub 3 m. tall, and the variety as a small tree 2.5 m. tall.

37. Piper aduncum L. Sp. Pl. 1:29. 1753.

Piper elongatum Vahl, Enum. Pl. 1:312. 1805, sensu Trelease in Contr. U. S. Nat. Herb. 26:36. 1927.
Piper celtidifolium H.B.K. Nov. Gen. & Sp. 1:50. 1815.

Artanthe adunca Miq. Comm. Phyt. 49. 1838.
Steffensia adunca Kunth, in Linnaea 13:633. 1939.
Artanthe celtidifolia Miq. Syst. Pip. 452. 1848.
Piper fatoanum C.DC. in Smiths. Misc. Coll. 71[6]:7. 1920.
Piper aduncum var. *laevifolium* C.DC. loc. cit. 8. 1920.
Piper elongatum var. *laevifolium* (C.DC.) Trel. in Contr. U. S. Nat. Herb. 26:37. 1927.
Piper intersitum Trel. in H. Daniel, Una Ascension Al Cerro de "La Vieja," Medellín, Colombia, 12. 1940, in part.
Piper intersitum var. *porcecitense* Trel. loc. cit. 13. 1940.

Shrub or small tree, mostly 3–9 m. tall, nodose; flowering internodes rather slender, short, rather sparsely pubescent glabrescent; leaves lanceolate to subelliptic, 4–8 or scarcely 10 cm. wide × 12–24 cm. long, apex sharp-acuminate, base inequilaterally rounded or cordulate, one side mostly 3–4 mm. shorter, pinnately nerved to the middle or upper third, the nerves 6–8 on each side, sharply ascending, the innermost meeting at the apex, gradually approximated downward with usually 2 or 3 on each side very near the base, scabrous and more or less pubescent above, at least along the nerves, commonly tardily somewhat rugulose, pubescent or glabrescent between the nerves and somewhat glandular-dotted beneath, the nerves commonly subappressed-hairy, drying firm, translucent, pellucid-dotted; petiole 3–8 plus 3–4 mm. long, pubescent, vaginate at the base; spikes 3–4 mm. thick × 8–15 cm. long, short-cuspidate, gradually curved or hooked; peduncle slender, 8–20 mm. long, mostly about 10–12 mm., puberulent; bracts triangular- or rounded-subpeltate, marginally fringed; fruit small, obovoid, more or less tri- or tetragonous, glabrous, stigmas sessile.

Fig. 6. *Piper aduncum*

West Indies and on the mainland through Central America and northern South America.

BOCAS DEL TORO: Cricamola Valley, vicinity of Almirante, *Cooper 531;* Isla Colón, alt. 0–120 m., *von Wedel 515.* CANAL ZONE: vicinity of Fort Sherman, *Standley 30941;* near Río Medio, Battery 46 Hill, *Miller 1770;* near old Fort Lorenzo, mouth of Río Chagres, *Piper 5985;* between Chagres Batteries and Fort San Lorenzo, Fort Sherman Military Reservation, *Maxon & Valentine 6992;* hills west of the canal, near Gatún, *Standley 27256;* alluvial bottom near Bohio, alt. 10–20 m., *Maxon 4766;* Madden Dam Road, *Miller 1803.* COLÓN: along the beach between Fató and Playa de Damas, *Pittier 3935, 3930;* forests around Porto Bello, alt. 5–100 m., *Pittier 2438.* PANAMÁ: near Tapia River, Juan Díaz region, *Maxon & Harvey 6671;* Tumba Muerto Road, near Panamá, *Standley 29803;* forests, on dry limestone, around Alhajuela, Chagres Valley, alt. 30–100 m., *Pittier 3510.*

37a. Piper aduncum var. **brachyarthrum** (Trel.) Yuncker, comb. nov.

Piper elongatum var. *brachyarthrum* Trel. in Contr. U. S. Nat. Herb. 26:37. 1927.
Piper Cuatrecasasi Trel. in Trab. Mus. Nac. Hist. & Jard. Bot. Madrid, Ser. Bot. 33:48. 1936.
Piper cumbricola Trel. loc. cit. 1936.
Piper cumbricola var. *montevagum* Trel. loc. cit. 1936.
Piper illudens Trel. loc. cit. 50. 1936.

Stems densely hirsute-villous; leaves moderately to densely soft-villous beneath. Occurs with the species.

Panamá: without locality, *Seemann 117*. chiriquí: vicinity of El Boquete, alt. 1000–1300 m., March 2–8, 1911, *Maxon 5139* (U. S. Nat. Herb., type). veraguas: vicinity of Santiago, alt. 50 m., *Allen 1010*. coclé: El Valle, *Miller 1815, 1816*. canal zone: Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper 5740*.

This is a widespread species which exhibits considerable variation in the size of the leaves and character and amount of pubescence. The rather slender, regularly curved spikes, short petioles, and somewhat longer peduncles are characteristic features. Variety *laevifolium* has slightly less scabrous leaves but otherwise agrees in all respects.

38. Piper hispidum Sw. Prodr. Veg. Ind. Occ. 15. 1788.

Piper scabrum Sw. Fl. Ind. Occ. 1:59. 1797.
Piper hirsutum Sw. loc. cit. 60. 1797.
Steffensia hirsuta Kunth, in Linnaea 13:640. 1839.
Steffensia scabra Kunth, loc. cit. 1839.
Artanthe hirsuta Miq. Syst. Pip. 446. 1844.
Artanthe scabra Miq. loc. cit. 447. 1844.
Piper erectamentum C.DC. in Smiths. Misc. Coll. 71^6:14. 1920.
Piper scabrilimbum C.DC. in Candollea 1:121, 276. 1923.
Piper Williamsii Trel. in Contr. U. S. Nat. Herb. 26:32. 1927.
Piper Killipi Trel. loc. cit. 33. 1927.
Piper Killipi var. *calderanum* Trel. loc. cit. 1927.
Piper sancti-felicis Trel. loc. cit. 35. 1927.
Piper rivi-vetusti Trel. in Ann. Mo. Bot. Gard. 24:186. 1937.
Piper barbirostre Trel. loc. cit. 27:288. 1940.
Piper casitense Trel. loc. cit. 289. 1940.
Piper cerro-puntoense Trel. loc. cit. 1940.
Piper konkintoense Trel. loc. cit. 293. 1940.
Piper Margaretae Trel. loc. cit. 1940.
Piper pervicax Trel. loc. cit. 296. 1940.
Piper pseudo-viridicaule Trel. var. *nievecitanum* Trel. loc. cit. 1940.

A shrub, up to 5–8 m. or more tall, rather nodose; flowering internodes moderately slender and rather short, hispid, sometimes glabrescent downward, hairs rigid, commonly more dense about the nodes, erect to reflexed, often of varying lengths; leaves elliptic or elliptic-ovate, 4–11 cm. wide × 11–20 or 25 cm. long, mostly 6–8 × 11–15 cm., apex acuminate, base obliquely inequilateral, one side 2–5 mm. shorter, mostly acute, the longer side usually rounded and obtuse, or in large leaves sometimes cordulate, pinnately nerved from the

lower half, the nerves 5–6 on each side or 7 in some large leaves, with cross-connecting nervules, sometimes rugescent in age, lepidote-scabrous, more or less hirtellous or hispid along the nerves above, the nerves beneath hispid-hirsute, commonly glandular-dotted, drying papery, translucent; petiole 5–10 plus 2–5 mm. long, hirtellous or hispid, vaginate at the base; spikes 3 mm. thick × 8–14 cm. long, mucronate; peduncle rather thick, scarcely 1 cm. long, hirtellous or hispid; bracts triangular-subpeltate, marginally fringed; fruit rather small, oblong-subpyramidal-trigonous, laterally compressed, papillate-puberulent at the truncate or depressed apex; stigmas small, sessile.

In a number of scarcely distinguishable forms throughout the West Indies, Central America, and much of South America.

Fig. 7. *Piper hispidum*

BOCAS DEL TORO: Río Cricamola, between Finca St. Louis and Kontintoë, alt. 10–50 m., *Woodson, Allen & Seibert 1894;* vicinity of Nievecita, alt. 0–50 m., *Woodson, Allen & Seibert 1829;* Daytona Farm, region of Almirante, *Cooper 165.* CHIRIQUÍ: vicinity of "New Switzerland," central valley of Río Chiriquí Viejo, alt. 1800–2000 m., *Allen 1365;* valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, alt. 1300–1900 m., *Seibert 192;* on trail to Cerro Punta, *White 52, 158;* Bajo Chorro, Boquete Distr., alt. 1800 m., *Davidson 58, 342;* El Boquete, alt. 1400–1650 m., *Killip 3549;* around Las Siguas Camp, southern slope of Cerro de la Horqueta, alt. 1700 m., *Pittier 3191;* Río Caldera, above El Boquete, alt. 1600 m., *Killip 3544;* vicinity of San Felix, alt. 0–120 m., *Pittier 5124;* vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., *Woodson, Allen & Seibert 843, 902, 978.* CANAL ZONE: Empire, *Miller 1868;* Barro Colorado Island, Gatún Lake, *Standley 31387.* PANAMÁ: Marraganti and vicinity, alt. 3–60 m., *Williams 986;* Indio, Madden Lake, *Miller 2064.* DARIÉN: Boca de Pauarandó, on Sambú River, alt. 20 m., *Pittier 5584*—some of the leaves on this specimen are up to 10–11 × 22–24 cm.

38a. PIPER HISPIDUM var. **trachydermum** (Trel.) Yuncker, comb. nov.

Piper trachydermum Trel. in Contr. U. S. Nat. Herb. 26:33. 1927.
Piper non-retrorsum Trel. loc. cit. 36. 1927.

Differs from the species in having the short, stout hairs on the upper internodes upwardly curved and more or less appressed.

Occurs with the species.

PANAMA: without location, 1859-60, *Hayes 791* (Herb. New York Bot. Gard., TYPE of *P. trachydermum*). COCLÉ: El Valle, valley floor and lower slopes, along highway, *Miller 1817*—leaves on this specimen are larger than usual. CANAL ZONE: Barro Colorado Island, Gatún Lake, alt. 120 m., *Standley 40872;* vicinity of Fort Sherman, *Standley 30121.* COLÓN: around Porto Bello, alt. 5–100 m., *Pittier 2429.* PANAMÁ: Río Tapia, *Standley 28208.*

38b. Piper hispidum var. **ellipticifolium** Yuncker, var. nov.

Caule hispido (pilis rigidis seorsum recurvantibus); foliis ellipticis, deorsum ad basem sensim angustatis, basi utrinque peracutis.

Stem hispid, the hairs rigid, upcurved; leaves elliptic, gradually narrowed to the base which is scarcely rounded and strongly acute on both sides, 7–8 cm. wide × 13–16 cm. long.

Known only from the type locality.

COCLÉ: Bismarck, above Penonomé, alt. 600–900 m., March 5–19, 1908, *Williams 343* (Herb. New York Bot. Gard., TYPE).

There is a great amount of variation in the size and to a lesser degree also the shape of the leaves on the specimen included here. All agree in having harshly scabrid leaves, hispid stems, and papillate-puberulent fruit. A study of the type specimens of the numerous species proposed by DeCandolle and by Trelease has failed to show any consistent characters upon which it is believed specific distinctions can be justified.

39. Piper vitabundum Trel. in Contr. U. S. Nat. Herb. 26:38. 1927.

Piper conscendens Trel. in Field Mus. Nat. Hist. Bot. Ser. 18:338. 1937.

Climbing; flowering internodes rather slender and long, moderately retrorse-strigose; leaves elliptic, apex acuminate, base inequilateral, one side 1–3 mm. shorter and acutish, the longer side acutish or obtuse, 3–4 cm. wide × 10–12 cm. long, pinnately nerved from the lower half, the nerves 4–5 on each side, lepidote, finely scabrous, and glabrous above, the nerves beneath appressed-pubescent, drying dark, subopaque; petiole about 5 plus 1–3 mm. long, pubescent, vaginate at the base; spikes 2–3 mm. thick × 7–8 cm. long; peduncle scarcely 1 cm. long, sparsely crisp-pubescent; bracts triangular-subpeltate, narrowly fringed; fruit oblong-subtetragonous, laterally compressed, papillate-puberulent at the top, stigmas sessile.

Known only from Changuinola Valley, Bocas del Toro.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 338*.

The vine-like habit of this species is distinctive. *P. conscendens* was based on the same collection as *P. vitabundum*.

40. Piper persubulatum C.DC. in Smiths. Misc. Coll. 71^6:4. 1920.

Shrub (?); flowering internodes rather slender and short, densely brown-villous, the hairs up to 1 mm. or more long; leaves lance-elliptic-oblong, with the midrib nearer one side, apex very narrowly long-acuminate, base subequally rounded, 5.5–8 cm. wide × 19–24 cm. long, pinnately nerved from the lower half, the nerves 6–7 on each side, with prominent cross-connecting nervules, the upper surface somewhat scabrous, loosely villous, the nerves rather densely so, marginally strongly long-ciliate, more densely dingy-hairy beneath, drying papery, subopaque; petiole scarcely 5 mm. long, densely villous, vaginate at the base; spikes 2 mm. thick × 10 cm. long; peduncle scarcely 5 mm. long, villous; bracts subpeltate, densely dingy-hairy; ovary elongated with the rachis, glabrous, stigmas sessile.

Known only from the following locality.

COLÓN: Loma de la Gloria, near Fató (Nombre de Dios), *Pittier 4240.*

The densely villous stems and leaves, long, slenderly acuminate leaves, and densely hairy bracts distinguish this species.

41. PIPER PERACUMINATUM C.DC. in Smiths. Misc. Coll. 71[6]:9. 1920.

A shrub or small tree, 2–3 m. tall; flowering internodes moderately short and stout, hirsute, the hairs of various lengths; leaves elliptic-obovate, apex narrowly sharp-acuminate, base inequilateral, cordulate, the longer side 2–4 mm. longer at the petiole and covering the petiole, 8–13 cm. wide × 16–27 cm. long, scabrous above and loosely villous or at least pubescent along the nerves, thinly long-hairy beneath, ciliate, somewhat rugescent or nearly smooth, pinnately nerved from the lower half, the nerves 6 or 7 on each side, drying rather thin, subtranslucent; petiole 5–10 plus 2–4 mm. long, densely hirsute, vaginate-winged to the blade; spikes 5 mm. thick × 10–13 cm. long; peduncle rather stout, 2 cm. long, with intermixture of short, stiff, and long, crisp hairs; bracts rounded- or triangular-subpeltate, fringed, pedicel villous; fruit oblong, compressed, rusty-hirtellous, stigmas sessile.

Panama.

CANAL ZONE: Chagres, *Fendler 269.* COLÓN: around Dos Bocas, Río Fató valley, alt. 40–80 m., *Pittier 4210;* Río Indio de Fató, *Pittier 4254.*

The rather large, scabrid, cordulate-based leaves, mixture of long and short stiff hairs, and hairy fruits distinguish this species.

42. PIPER ERUBESCENTISPICUM Trel. in Ann. Mo. Bot. Gard. 27:291. 1940, as *erubescentispica.*

A shrub, 2 m. tall, nodose; flowering internodes rather short and slender, evanescently villous; leaves rhombic-elliptic, apex sharp-acuminate, base inequilateral, cordulate, one side 2–4 mm. shorter, 4–6.5 cm. wide × 10–14 cm. long, pinnately nerved from the lower half, the nerves 4–5 on each side, with rather prominent cross-connecting nervules, harshly scabrous, sparsely villous above, the hair bases enlarged, whitish, loosely villous beneath, at least along the nerves, the hairs more or less erect, up to 1 mm. or more long, marginally ciliate, young leaves woolly-villous when unfolding, drying papery, translucent; petiole scarcely 5 plus 2–4 mm. long, at first villous, vaginate at the base; spikes red, as reported, 2 mm. thick × 6 cm. long; peduncle about 5 mm. long, glabrescent; bracts glabrous, triangular-subpeltate, dorsally somewhat projected and callose, slightly ciliate beneath; fruit not developed, stigmas sessile.

Bocas del Toro.

BOCAS DEL TORO: vicinity of Nievecita, alt. 0–50 m., *Woodson, Allen & Seibert 1817;* Sansan Swamp, region of Almirante, *Cooper 190.*

The villous, more or less rhombic-elliptic, scabrous leaves, red spikes, and irregularly shaped bracts distinguish this species.

43. Piper culebranum C.DC. in Candollea 1:121, 243. 1923.

A shrub or small tree, 2 m. tall; upper internodes comparatively short and slender, loosely to moderately crisp-villous; leaves elliptic, elliptic-oblanceolate or elliptic-subobovate, apex acutely long-acuminate, base 3–5 mm. shorter on one side, obtuse, or longer side cordulate, 5–7 or sometimes 9 cm. wide × 15–20 cm. long, pinnately nerved from the lower half, the nerves 4–5 on each side, with cross-connecting and anastomosing nervules, sparsely white-villous glabrescent above, mostly crisp-villous and slightly scabrous beneath, the nerves more densely so, drying rather thin, green, somewhat glossy, translucent; petiole mostly about 5 plus 3–5 mm. long, crisp-villous, vaginate at the base; spikes 4 mm. thick × 7–9 cm. long; peduncle 1 cm. long, crisp-villous; bracts round-triangular-subpeltate, with a wide, dense yellow fringe; fruit subcylindrical, truncate; stigmas sessile.

Central Panama.

canal zone: Empire, *Miller 1866;* near Fort Randolph, *Standley 28622, 28667.* colón: along the Río Culebra, above Santa Isabel, near sea-level, *Pittier 4154;* between France Field, Canal Zone and Catival, *Standley 30375.* panamá: Juan Díaz, *Standley 30611;* along Río Juan Díaz above Juan Díaz, alt. 30 m., *Allen 034.*

There is considerable variation in the size of the leaves on the specimens included here, especially Miller's *No. 1866,* but they agree very well otherwise, and it is believed they all represent the same species.

44. Piper viridicaule Trel. in Contr. U. S. Nat. Herb. 26:32. 1927.

A shrub, 2 m. tall, branches subdichotomously forked; flowering internodes slender, elongating downward, villous, the hairs up to 1 mm. or more long; leaves lance-elliptic, apex sharp-acuminate, base inequilateral, cordulate, one side 2–4 mm. longer and covering the petiole, 3–4.5 cm. wide × 9–12 cm. long, pinnately nerved from the lower half, the nerves 4 or occasionally 5 on each side, with slender cross-connecting nervules, sparsely villous and harshly scabrous above, paler beneath and appressed-villous, especially along the nerves, marginally long-ciliate, pale-glandular-dotted beneath, drying thin, translucent; petiole 5–20 plus 2–4 mm. long, villous, vaginate at the base; spikes unknown.

Known only from Barro Colorado Island.

canal zone: Barro Colorado Island, Gatún Lake, *Standley 31402.*

The absence of inflorescence on the only specimen known of this species makes its position questionable. The vegetative characters, especially the villous twigs and leaves, distinguish it from any other known species.

45. Piper pervelutinum Trel. in Contr. U. S. Nat. Herb. 26:39. 1927.

Shrub (?), nodose; flowering internodes short, rather stout, densely subvillous; leaves lance-oblong, apex subacuminate, base inequilateral, rounded, obtuse, one side 2–5 mm. shorter, the upper surface rugose, scabrous, hirsute, especially along the nerves, dull, densely dingy-villous and slightly scabrous beneath, not ciliate, pinnately nerved from the lower half, the nerves 6–7 on each side, impressed above,

gradually approximated downward, drying rather thick, opaque; petiole 8–10 plus 2–5 mm. long, densely dingy-villous, clasping and vaginate at the base; spikes as yet immature, 2 mm. thick × 1.5 cm. long; peduncle short, densely hairy; bracts round-subpeltate, fringed, the dorsal hairs much longer; ovary not formed.

Known only from the one specimen.

PANAMA: without locality, *Hayes 796*.

46. PIPER **variitrichum** Yuncker, sp. nov.

Frutex 1–2 m. altus, caulibus nodosis; internodiis floriferis gracilibus conferte atro-pubescentibus; foliis ovato-ellipticis, apice acute acuminatis, basi inaequilateraliter obliquis, latere angusto obtuso vel acuto, latere lato rotundato cordulato, supra conferte scabridis, a tertio supero deorsum pinnatim venosis, venis utrinque 5–6, supra hispidis subtus pubescentibus, ad venas sat conferte hirsutis, pilis erectis brevioribus longioribusque intermixtis; petiolo 1–1.5 cm. longo, conferte hirsuto, deorsum vaginato; spicis immaturis 2 mm. crassis, 4 cm. longis apiculatis; pedunculo 5 mm. longo conferte pubescente; bracteis rotundato-subpeltatis fimbriatis.

Fig. 8. *Piper variitrichum*

Shrub, 1–2 m. tall, nodose; flowering internodes slender, lengthening downward, densely dingy-pubescent; leaves ovate-elliptic, apex narrowly attenuately acuminate, base inequilaterally oblique, essentially equal length at the petiole, the narrower side narrowing downward, obtuse or acutish, the broader side rounded, cordulate, 6–8 cm. wide × 15–23 cm. long, harshly scabrous above, less so beneath, pinnately nerved below the upper third, the nerves 5–6 on each side, with slender, cross-connecting nervules, glandular-dotted and hispid above, pubescent beneath with the nerves rather densely staring-hairy with a mixture of various length hairs, scarcely ciliate, drying rather thin, translucent; petiole 1–1.5 cm. long, densely hairy, vaginate toward the base; spikes as yet young, 2 mm. thick × 4 cm. long, apiculate; peduncle 5 mm. long, densely pubescent; bracts round-subpeltate, fringed, with a few dorsal hairs longer; ovary and fruit not developed.

Known only from the type locality.

DARIÉN: Chepigana Distr., Caña-Cuasi Trail (Camp 2), alt. 600 m., March 9, 1940, *Terry & Terry 1428* (Herb. Missouri Bot. Gard., TYPE).

The comparatively large leaves, narrowly acuminate apex, the margins essentially equal at the petiole, and various length hairs on the nerves beneath distinguish this species.

47. PIPER CHANGUINOLANUM Trel. in Contr. U. S. Nat. Herb. 26:37. 1927.

A nodose shrub with scabrous twigs and leaves; flowering internodes short and comparatively slender, finely hispid and granular; leaves inequilateral, narrowly elliptic-oblong, apex acuminate, base 2–4 mm. shorter on one side and acute, the longer side rounded, cordulate, 3–4 cm. wide × 12–15 cm. long, pinnately nerved from below the middle, the nerves 5–6 on each side, rather slender but conspicuous beneath, with slender cross-connecting nervules, slightly rugose in age, the nerves above hispidulous, paler and granular-dotted beneath and appressed-pubescent on the nerves, appressed-hispidulous ciliate, drying papery, translucent; petiole scarcely 5 plus 2–4 mm. long, hispid, vaginate at the base; spikes 3 mm. thick × 8–10 cm. long; peduncle scarcely 1 cm. long, subappressed-hispid; bracts rounded-triangular-subpeltate, thinly stiff-ciliate, the anterior setae longer; fruit oblong, laterally-compressed, apex depressed-truncate, granulate or essentially glabrous, stigmas sessile.

Known only from Changuinola Valley, Bocas del Toro.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 233*.

48. PIPER VILLIRAMULUM C.DC. in Smiths. Misc. Coll. 71[6]:11. 1920.

Piper bocasense Trel. in Field Mus. Nat. Hist. Bot. Ser. 18:333. 1937.
Piper yapeanum Trel. in Ann. Mo. Bot. Gard. 25:827. 1938.

A shrub or small tree, commonly 2–3 m. tall; flowering internodes moderately slender, moderately to rather densely villous; leaves ovate or elliptic-ovate, apex acuminate, base inequilaterally oblique, one side 3–5 mm. shorter and obtuse, the longer side rounded, cordulate, mostly 5–8 cm. wide × 13–18 cm. long, occasional leaves somewhat larger, scabrous on both sides but more harshly so above, moderately appressed-hairy on both sides, becoming somewhat builulate, pinnately nerved from the lower half, the nerves 6 or 7 on each side, drying rather thin, translucent; petiole 5–10 plus 3–5 mm. long, vaginate at the base, moderately to densely villous; spikes 3 mm. thick × 7–9 cm. long; peduncle rather stout, scarcely 5 mm. long, hairy; bracts rounded-triangular-subpeltate, fringed, the hairs comparatively short, coarse and somewhat rigid; fruit tetragonous, laterally compressed, glabrous or obscurely papillate at the apex, stigmas sessile.

Panama.

BOCAS DEL TORO: region of Almirante, *Cooper 407*; Changuinola Valley, *Dunlap 234*; vicinity of Chiriquí Lagoon, *von Wedel 1215*; Water Valley, *von Wedel 608, 1777, 2000*; Shepherd Island, *von Wedel 2679*—this specimen is more rugose than usual. CANAL ZONE: Río Pedro Miguel, near East Paraíso, *Standley 20066*; around El Paraíso, alt. 30–100 m., *Pittier 2534*; Corozal, *Stevens 124*; *Riley 138*; along the old Las Cruces Trail, between Fort Clayton and Corozal, *Standley 20100*; between Miraflores and Corozal, alt. 20–30 m.,

Pittier 2193; Las Cascadas Plantation, near Summit, *Standley 25692, 25701, 26012;* Summit, *Standley 26937;* Cerro Gordo, near Culebra, *Standley 25998;* Balboa, *Standley 26073, 29267;* Gamboa, *Standley 28522;* Empire, *Miller 1869;* Empire to Mandinga, *Piper 5514;* vicinity of Ancón, *Piper 6028; Bro. Celestine 32;* Río Agua Salud, near Frijoles, *Piper 5867;* near Río Medio, Madden Dam Road, *Miller 1768, 1769, 1771, 1802;* vicinity of Madden Dam, near Río Chagres, alt. 50–75 m., *Seibert 549;* near old Fort Lorenzo, mouth of Río Chagres, *Piper 5971.* COLÓN: Loma de la Gloria, near Fató (Nombre de Dios), alt. 10–104 m., *Pittier 4083.* PANAMÁ: Sabana de Juan Corso, near Chepo, alt. 60–80 m., *Pittier 4537;* along the Corozal Road, near Panamá, *Standley 26843;* Juan Díaz, *Standley 30623;* Río Tapia, *Standley 28134;* 3 miles east of Juan Díaz, alt. 75 m., *Killip 3123;* Bella Vista, *Macbride 2732;* Camino de La Granja, *Bro. Heriberto 165.* DARIÉN: near mouth of Río Yapé, alt. 20 m., *Allen 351.*

48a. PIPER VILLIRAMULUM var. GAMBOANUM (C.DC.) Trel. in Contr. U. S. Nat. Herb. 26:36. 1927.

Piper gamboanum C.DC. in Candollea 1:249. 1923.
Piper hispidum Sw. var. *gamboanum* C.DC. in Smiths. Misc. Coll. 71^6:12. 1920.
Piper gamboanum var. *yapense* Trel. in Ann. Mo. Bot. Gard. 27:291. 1940.

Leaves 2–4 or occasionally up to 4.5–5 cm. wide.

Occurs with the species.

CANAL ZONE: around Gamboa, alt. 20–100 m., *Pittier 3410;* Corozal, *Stevens 116, 117;* foot of Corozal Hill, *Miller 1788;* along the old Las Cruces Trail, between Fort Clayton and Corozal, *Standley 29048;* Las Cascadas Plantation, near Summit, *Standley 29630;* Obispo, *Standley 31794.* PANAMÁ: near the big swamp, east of Río Tecumen, *Standley 26598;* between Las Sabanas and Matías Hernández, *Standley 31818.* DARIÉN: vicinity of Yapé, *Allen 854.*

The appressed-villous, scabrous, bullulate leaves, and short, stout peduncles characterize this species and distinguish it from *P. taboganum* in which the leaves are less scabrous, scarcely bullulate, more densely hairy, and with longer peduncles. The young spikes of *P. taboganum* are also usually very short and bristly from the erect bract hairs. The type of *P. yapeanum* is reported as a tree 15 m. tall. The type specimen agrees in all other respects with those reported as being much smaller plants.

49. PIPER TABOGANUM C.DC. in Smiths. Misc. Coll. 71^6:4. 1920.

Piper obaldianum C.DC. loc. cit. 7. 1920.
Piper dumeticola C.DC. var. *panamense* C.DC. loc. cit. 1920.
Piper pallidibracteum C.DC. loc. cit. 8. 1920.
Piper salinasanum C.DC. var. *parvifolium* C.DC. in Ann. Conserv. & Jard. Bot. Genève 21:234. 1920.
Piper barbinerve Trel. in Contr. U. S. Nat. Herb. 26:35. 1927.
Piper Bigelovii Trel. loc. cit. 23. 1927.
Piper subdilatatum Trel. loc. cit. 35. 1927.
Piper chagresianum Trel. loc. cit. 37. 1927.
Piper breve C.DC. in Trel. loc. cit. 38. 1927.
Piper breve var. *pallidineurum* Trel. loc. cit. 1927.
Piper breve var. *pseudo-dumeticola* Trel. loc. cit. 1927.
Piper breve var. *bellae-vistae* Trel. loc. cit. 39. 1927.
Piper breve var. *divaricatum* Trel. loc. cit. 1927.
Piper breve var. *pseudo-fatoanum* Trel. loc. cit. 1927.
Piper cayazasense Trel. in Ann. Mo. Bot. Gard. 25:826. 1938.

Piper amphibium Trel. loc. cit. 27:288. 1940.
Piper insulicolum Trel. loc. cit. 293. 1940.
Piper tabernillanum Trel. var. *anconense* Trel. loc. cit. 298. 1940.
Piper tembladorense Trel. in Ll. Williams, Expl. Bot. Guyana Venez. 177. 1942 (Serv. Bot. Minist. Agr. y Cria).

A shrub, mostly 1–3 m. tall; upper internodes rather short and slender, soft-villous, crisp-pubescent, or subhispid, more or less canescent; leaves rhombic-subobovate, elliptic, or less commonly lance-elliptic, mostly 4–6 cm. wide × 10–15 cm. long, or occasional leaves up to 9 × 22 cm., apex acuminate, narrowed downward to the inequilaterally rounded base, one side commonly 2–5 mm. shorter, the longer side obtuse or cordulate, pinnately nerved from below the middle, the nerves 5–6 or sometimes 7 on each side, often slightly rugescent near the margin or toward the base, crisp-hirtellous or subhispid above with the midrib densely so, somewhat scabrous from the persistent hair bases, soft-pubescent beneath, the nerves usually densely so, the hairs appressed, drying rather thin, translucent; petiole 5–10 or occasionally up to 20 plus 2–5 mm. long, densely hairy, vaginate commonly to the middle or above, the groove smooth or hairy within; spikes scarcely 1 cm. long when young and more or less bristly from the suberect bract hairs, becoming 3–4 mm. thick × 4–10 cm. long, commonly apiculate; peduncle mostly 5–10 or occasionally up to 20–25 mm. long, pubescent; bracts rounded or triangular-subpeltate, marginally fringed, the hairs rather stiff, those on the dorsal margin usually longer and suberect in young spikes; fruit oblong-subtrigonous, glabrate or slightly papillate when young; stigmas small, sessile.

Northern South America and Panama.

Panamá: without locality, *Bigelow s. n.*; *Née 358, 365*. Chiriquí: Boquete District, Boquete, alt. 1140 m., *Davidson 617*. Veraguas: trail between Cañazas and the foot of the Cordillera Central, headwaters of Río Cañazas, alt. 300–600 m., *Allen 185*. Coclé: vicinity of Olá, alt. 100–350 m., *Pittier 5034*; El Valle de Antón and vicinity, alt. 500–700 m., *Seibert 436*; El Valle, *Miller 1818, 1819*—small-leaved specimens—*1820*; between Aguadulce and Antón, alt. 15–50 m., *Woodson, Allen & Seibert 1222*; vicinity of Santa Clara beach, *Woodson, Allen & Seibert 1705*; between Las Margaritas and El Valle, *Woodson, Allen & Seibert 1306, 1728*. Canal Zone: Empire, *Miller 1864, 1869*; Empire to Mandinga, *Piper 5523*; near old Fort Lorenzo, mouth of Río Chagres, *Piper 5944*; between Chagres Batteries and Fort San Lorenzo, Fort Sherman Reservation, *Maxon & Valentine 6086*; vicinity of Fort Sherman, *Standley 30918, 30982, 31140*; western slope of Ancón Hill, vicinity of Balboa, alt. 20–75 m., *Seibert 118, 119, 300*; *Woodson, Allen & Seibert 1327*; *Standley 25203, 26382, Killip 12078*; Balboa, *Standley 25420, 25603, 25565*; 2 miles west of Balboa, *Correll 12261*; Las Sabanas, *Bro. Celestine 110*; *Riley 116*; Cocli, *Riley 127*; Matachin, *Cowell 204*; foot of Corozal Hill, *Miller 1701*; Corozal, *Standley 27341*; near Fort Randolph, *Standley 28659*; *Maxon & Harvey 6504, 6543*; Fort Kobe road, *Woodson, Allen & Seibert 1412*; Brazos Brook Reservoir, *Stevens 752*; Culebra, *Stevens 903*; alt. 50–150 m., *Pittier 3445*; around Gamboa, in thickets, alt. 40–80 m., *Pittier 3709*; *Standley 28374, 28481*; between Gamboa and Cruces, alt. 50–80 m., *Pittier 3787*; France Field, *Stevens 981*; Margarita Swamp, south of France Field, *Maxon & Valentine 7055*; between France Field, Canal Zone and Cativa1, Colón, *Standley 30164*; Mount Hope Cemetery, *Standley 28776*; Obispo, *Standley 31764*; Juan Mina, *Piper 5692*; Cerro Gordo, near Culebra, *Standley 25075, 26018*; Chivi-Chivi Trail, 2 miles above Red Tank, *Maxon & Harvey 6591*. Colón: Chagres, *Fendler 268*; Río Culebra, above Santa Isabel, *Pittier 4148*; Río Indio de Fató, near sea-level, *Pittier 4271*; along the beach between Fató and Playa de Damas, *Pittier 3923, 3930*. Panamá: near Matías Hernández, *Standley 28957*;

near Las Sabanas, *Standley 40779;* between Las Sabanas and Matías Hernández, *Standley 31832;* Río Tapia, *Standley 28103;* near Tapia River, Juan Díaz Region, *Maxon & Harley 6620, 6626;* Sabana de Juan Corso, near Chepo, alt. 60–80 m., *Pittier 4539;* Río Tecumen, *Standley 29451;* near big swamp east of Río Tecumen, *Standley 26551;* near Punta Paitilla, *Standley 26303; Stevens 340;* Juan Díaz, *Standley 30637;* Tumba Muerto Road, near Panamá, *Standley 29724;* Bella Vista, at sea-level, *Killip 12045, 12004; Piper 5331;* vicinity of Juan Franco Race Track, near Panamá, *Standley 27713, 27734, 27777;* Taboga Island, *Woodson, Allen & Seibert 1527; Standley 27019, 27920; Miller 1845, 1846*—a large-leaved specimen—, *1847;* alt. 90 m., *Collenette 487; Killip 3194; Pittier 3529;* Taboguilla Island, *Miller 2003;* Perlas Archipelago, San José Island, *Johnston 687, 1019, 1404; Erlanson 376*—this specimen differs in having more elliptic-ovate leaves scarcely narrowed toward the base, but it agrees very well in other characters; Trapeche Island, *Miller 1908, Allen 2618;* Saboga Island, *Miller 1951*—a large-leaved specimen—*1952.* SAN BLAS: forests around Puerto Obaldía, alt. 0–50 m., *Pittier 4366, 4396*—a large-leaved specimen. DARIÉN: Chepigana District, Caña-Cuasi Trail, alt. 600 m., *Terry & Terry 1428.*

This species is one of the most common in Panama where it occurs in a great variety of scarcely differentiable forms. It appears to be rather closely related to *P. mollicomum* of Brazil, from which it differs, however, because of its mostly less venulose and more finely rugescent leaves which have the margins less rounded below the middle, and with generally shorter peduncles. The type specimen of *P. mollicomum* has not been examined by the writer and the above contrast is based on notes and sketches made by the late Professor Trelease from specimens in European herbaria. There is a considerable range in size and amount of pubescence shown by the leaves, often on the same specimen. The contrast between large-leaved and small-leaved specimens is very great. Other specimens, however, show intergradations in size to such an extent that it does not seem advisable to establish or maintain varieties based on this character alone. The type of *P. Bigelovii* is a rather poor specimen which appears to agree well with this species although it is somewhat more tomentose than usual for most of the specimens included.

50. PIPER PSEUDO-CATIVALENSE Trel. in Contr. U. S. Nat. Herb. 26:34. 1927.

Shrub, 2 m. tall; flowering internodes rather slender and somewhat elongate, crisp-pubescent; leaves elliptic or elliptic-ovate, apex bluntly short-acuminate, mucronate, base inequilaterally rounded, cordulate, larger leaves strongly so, equal at the petiole or one side about 2 mm. shorter, mostly 5–6 cm. wide × 10–13 cm. long, pinnately nerved from the lower half, the nerves 4–5 on each side, with cross-connecting-anastomosing nervules, scabrous, crisp-hairy on both sides, the nerves more densely so, the hairs on the nerves beneath upcurved, drying papery, translucent; petiole about 10 plus 2 mm. long, crisp-pubescent, vaginate to the middle or above; spikes as yet very young, bristly with the erect bract hairs; peduncle pubescent; ovary or fruit not developed.

Known only from the following locality.

COLÓN: France Field, Canal Zone, and Cativa1, *Standley 30399.*

The elliptic or somewhat ovate leaves, hairy on both sides, and with the base rounded-cordulate on both sides, and bristly young spikes distinguish this species. It is apparently closely related to *P. taboganum* but differs because of the shape of the leaf, and more rounded cordulate base.

51. Piper lucigaudens C.DC. in Smiths. Misc. Coll. 71[6]:10. 1920.

Piper pseudo-viridicaule Trel. in Ann. Mo. Bot. Gard. 27:296. 1940.

A shrub or small tree, up to 3–4 m. tall, nodose; flowering internodes somewhat zigzag, slender and rather short, granular, sparingly crisp-pubescent; leaves elliptic or elliptic-oblanceolate, the midrib somewhat nearer one side, apex narrowly attenuately acuminate, base inequilateral, one side 2–5 mm. shorter, acute or the longer side more rounded and obtusish, 4–6 cm. wide × 13–17 cm. long, somewhat scabrous, pinnately nerved from the lower half, the nerves 4–5 on each side, with cross-connecting-anastomosing nervules, glabrous above, hirsute along the nerves beneath, the hairs suberect, mostly 0.5 mm. or more long, drying papery, green above, paler and glandular-dotted beneath, translucent; petiole about 5 plus 2–5 mm. long, somewhat hirsute, vaginate at the base; spikes as yet young, 2–3 mm. thick × 8–10 cm. long, peduncle up to 1 cm. long, granular, glabrous; bracts rounded- or triangular-subpeltate, narrowly and sparsely fringed; ovary or fruit not developed.

Panama.

CANAL ZONE: forest along the Río Indio de Gatún, near sea-level, *Pittier 2791, 2791a;* near Río Medio, *Miller 1766;* Barro Colorado Island, *Standley 31288, 31387.*

51a. Piper lucigaudens var. **Alleni** (Trel.) Yuncker, comb. nov.

Piper Alleni Trel. in Ann. Mo. Bot. Gard. 25:826. 1938, not C.DC. 1910.

Tree 7 m. tall; flowering internodes more densely subhispid; leaves somewhat larger, hairs beneath on midrib appressed, less than 0.5 mm. long.

Known only from the type locality.

DARIÉN: trail between Pinogana and Yavisa, alt. 15 m., *Allen 270* (Herb. Univ. Ill., TYPE)—"Roots used by Indians to deaden pain, leaves used as snake bite remedy."

The specimen upon which *P. pseudo-viridicaule* was based is sterile. It agrees very well in its vegetative characters with the others included here, and it is believed to be the same.

52. Piper Storkii Trel. in Contr. U. S. Nat. Herb. 26:32. 1926.

Shrub (?), nodose, nearly glabrous; flowering internodes slender and short, granular, sparsely pubescent when young; leaves elliptic or lance-elliptic, the midrib nearer one side, apex attenuately acuminate, base strongly inequilateral, one side 2–3 mm. shorter, acute, the longer side rounded, obtuse, pinnately nerved from the lower half, the nerves 4–5 on each side, approximated downward, with cross-connecting-anastomosing nervules, 4–5 cm. wide × 14–16 cm. long, glabrous and somewhat scabrid above, very obscurely appressed-pubescent beneath, at least along the nerves, drying thin, green, translucent; petiole about 5 plus 2–3 mm. long, granular, glabrous, vaginate at the base; spikes as yet young, 2 mm. thick × 6 cm. long; peduncle scarcely 5 mm. long, stout, glabrous; bracts triangular-subpeltate, glabrous or with a few, short, ventral hairs; ovary and fruit not matured.

Known only from Bocas del Toro.

BOCAS DEL TORO: Rubber Tree Station, *Stork 124.*

The thin, nearly glabrous leaves, and essentially glabrous bracts characterize this species.

53. PIPER WAGNERI C.DC. in DC. Prodr. 16[1]:302. 1869.

Piper minutispicum C.DC. in Smiths. Misc. Coll. 71[6]:1. 1920.
Piper Wagneri var. *minutispicum* Trel. in Contr. U. S. Nat. Herb. 27:29. 1927.

A glabrous, nodose shrub; upper internodes relatively short and slender; leaves lance- or ovate-elliptic, apex moderately acuminate, base subequilateral, the margin equal at the petiole or with one side commonly 1–5 mm. shorter, acute or occasionally with the longer side subcordulate, 4–7 cm. wide × 10–14 cm. long, pinnately nerved from below the middle, the nerves 3–5 on each side, with fine, cross-connecting-anastomosing nervules, glandular-dotted beneath, drying rather papery, translucent; petiole 10–25 plus 1–5 mm. long, vaginate to the blade; spikes up to 4 mm. thick × 9 mm. long, mucronate; peduncle 5–8 mm. long; bracts concave-inflexed, glabrous; ovary glabrous, stigmas sessile.

Southwestern Panama.

CHIRIQUÍ: *Wagner;* oak-palm forest above Sabana de El Salto, above El Boquete, alt. 1500–1750 m., *Pittier 3116.*

DeCandolle described *P. minutispicum* as dioecious. The spikes on the type are very young and, as in young spikes generally, the ovary is scarcely developed. It is believed that specimens with mature spikes will show that the flowers are perfect. Otherwise, the types of *P. Wagneri* and *P. minutispicum* appear to be the same species. The glabrous stems and leaves and very short spikes are distinctive characters.

54. PIPER DUNLAPI Trel. in Contr. U. S. Nat. Herb. 26:23. 1927.

Shrub (?), nodose, glabrous; flowering internodes rather short and slender, glandular-dotted; leaves ovate or lance-ovate, apex gradually sharp-acuminate, base inequilateral, acute, or equilaterally rounded and obtuse, 3.5–5.5 cm. wide × 10–13 cm. long, pinnately nerved from below the upper third, the nerves about 4–5 on each side, with faint cross-connecting-anastomosing nervules, strongly glandular-dotted on both sides, drying rather thick, narrowly revolute, subtranslucent, glossy above, dull beneath; petiole 1–1.5 cm. long, vaginate at the base, or on larger leaves to the blade; spikes as yet immature, somewhat curved, apiculate, 3 mm. thick × 2–3 cm. long; peduncle slender, scarcely 1 cm. long; bracts round- or subquadrangular-subpeltate, densely yellow-fringed, the fringe hairs filiform; ovary and fruit not developed.

Known only from the following locality.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 231.*

The glabrous stems and leaves, short spikes, and densely yellow-fringed bracts distinguish this species. It resembles *P. hirtellipetiolum* var. *subtrinerve* to a considerable extent but differs because of its more rounded floral bracts which are scarcely umbonate when young, and with more filiform fringe hairs. The Gray Herbarium specimen, obviously the same collection as that of the type in the U. S. National Herbarium, has scarcely glandular-dotted leaves.

55. Piper palmasanum C.DC. in Smiths. Misc. Coll. 71[6]:3. 1920.

A shrub; flowering internodes moderately slender, elongating downward, from very sparingly soft-pubescent quickly glabrescent; leaves ovate-lanceolate, apex gradually sharp-acuminate, base subequilaterally rounded or with one side 1–2 mm. shorter at the petiole, obtuse or abruptly acutish at the petiole, 3–5.5 cm. wide × 10–15 cm. long, pinnately nerved from below the middle, the nerves about 4 on each side, gradually closer together downward, impressed above, raised beneath, with cross-connecting-anastomosing nervules, glabrous above, the nerves beneath appressed-hairy, obscurely glandular-dotted beneath, drying firm, subtranslucent; petiole 5–15 mm. long, sparsely pubescent glabrescent, vaginate-winged to the middle; spikes yellow, as yet young, 2 mm. thick × 2 cm. long, mucronate; peduncle 5–10 mm. long, sparsely pubescent; bracts triangular-subpeltate, yellow-fringed; ovary and fruit not developed.

Known only from Cuesta de Las Palmas, Chiriquí.

Chiriquí: humid forest of Cuesta de Las Palmas, southern slope of Cerro de la Horqueta, alt. 1700–2100 m., *Pittier 3225*.

The relatively small, yellow spikes, and the character of the pubescence characterize this species.

56. Piper reptabundum C.DC. in Bot. Gaz. 70:169. 1920.

"Repent or scandent," glabrous; flowering internodes slender and short, granular-scurfy; leaves strongly inequilaterally, somewhat falcately, oblong-elliptic, the margin on one side quite straight and subparallel with the midrib to near the apex, the other side strongly curved from the base to the tip, apex sharply acuminate, base inequilateral with one side about 2 mm. shorter, the longer side obtuse or cordulate-auriculate and covering the petiole, 3.5–5.5 cm. wide × 13–20 cm. long, pinnately nerved from below the upper third, the nerves 4–6 on each side, strongly curved toward the apex, with strong cross-connecting veinlets and finely nervulose with anastomosing nervules, finely granular beneath, drying rather firm, translucent; petioles nearly obsolete, 1–2 plus 2 mm. long, scurfy; spikes 2 mm. thick × 4–8 cm. long, somewhat curved; peduncle slender, 4–7 cm. long; bracts small, triangular-subpeltate, smooth or granular-papillate; fruit obpyriform-trigonous, granular-papillate; stigmas sessile.

Costa Rica and adjacent Panama.

Bocas del Toro: Sibubi Falls, Sixaola Valley, *Rowlee & Rowlee 392* (Cited as *372* by Trelease in Contr. U. S. Nat. Herb. 26:38. 1927).

The subarcuate leaf shape and very long peduncles strongly characterize this species.

57. PIPER CHIRIQUINUM C.DC. in Smiths. Misc. Coll. 71[6]:2. 1920.

Piper paso-anchoense Trel. in Ann. Mo. Bot. Gard. 27:295. 1940.

A shrub, 2–3 m. tall, glabrous, nodose; flowering internodes rather slender and short, smooth or with round lenticels; leaves ovate or lance-ovate, apex bluntly acuminate, base mostly rounded, acute or obscurely and shallowly cordate, abruptly contracted onto the petiole, 3.5–8 cm. wide × 8–14 cm. long, pinnately nerved from below the upper third, the nerves 3–4 on each side in small leaves or 4–5 in larger leaves, with 2 or 3 pairs from near the base and 1 or 2 pairs above, with a few shorter intermediates and cross-connecting-anastomosing nervules, drying firm, pale green, translucent; petiole 10–25 mm. long, vaginate at the base or occasionally to about the middle; spikes 2–3 mm. thick × 5–8 cm. long, usually mucronate; peduncle 5–10 mm. long; bracts rhomboid-subpeltate, umbonate, submarginally ciliolate; fruit obpyramidal-trigonous, glabrous, stigmas sessile.

Panama.

CHIRIQUÍ: pastures around El Boquete, alt. 1000–1300 m., *Pittier 2930; Maxon 4944; Davidson 725;* forests along the Río Ladrillo and vicinity, above El Boquete, alt. 1200–1300 m., *Maxon 5557, 5558;* trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, alt. 1500–2000 m., *Allen 1579.*

This species bears some resemblance to *P. aequale* from which it is to be distinguished, however, because of the leaf shape and type of venation. The type of forma *b* has smaller leaves but the range in size of leaves on the different specimens is so great that it is not believed that it merits recognition.

58. PIPER TENUIMUCRONATUM C.DC. in Smiths. Misc. Coll. 71[6]:12. 1920.

A glabrous shrub, 1–3 m. tall; flowering internodes slender and rather short, pale-granular or glandular-dotted downward; leaves lance-ovate or elliptic, apex attenuately rather long-acuminate, commonly bristle-pointed, base subequilaterally acute, 3–5.5 cm. wide × 8–12 cm. long, pinnately nerved from below the middle, the nerves 3–4 on each side, with cross-connecting-anastomosing nervules, finely granular- or glandular-dotted beneath, drying green above, paler beneath, rather thin, translucent; petiole 10–15 mm. long, vaginate at the base only; spikes 3 mm. thick × 4–7 cm. long, apiculate; peduncle 1–2 cm. long; bracts triangular- or lunulate-subpeltate, margin conspicuously white-fringed; fruit globose or ovoid, laterally somewhat compressed; stigmas 3, sessile.

Panama.

CHIRIQUÍ: humid forest around Los Siguas Camp, southern slope of Cerro de la Horqueta, alt. about 1700 m., *Pittier 3185; Maxon 5421;* Bajo Chorro, Boquete District, alt. 1800 m., *Davidson 321, 719;* forest along the Río Ladrillo and vicinity, about El Boquete, alt. 1200–1300 m., *Maxon 5395;* Monniche Trail, Chiriquí Volcano, alt. 1700 m., *Killip 3523.*

The shape, rather prominent bristle tips, and nervation of the leaves characterize this species.

59. Piper septuplinervium (Miq.) C.DC. in DC. Prodr. 16[1]:313. 1869.

Artanthe septuplinervia Miq. in Seem. Bot. Voy. Herald, 199, *pl. 40.* 1854.

Shrub (?), glabrous, strongly nodose; flowering internodes short and slender, smooth or somewhat scurfy-granular; leaves lance- or oblong-ovate, apex rather long and sharply acuminate, base equilateral, rounded, obtuse, 3–4.5 cm. wide × 9–12 cm. long, pinnately nerved below the upper third, the nerves 4–5 on each side, prominent beneath, with fine cross-connecting-anastomosing nervules, drying pale green, firm, narrowly revolute, scarcely glandular-dotted; petiole about 5 mm. long, channelled above, vaginate at the very base only; spikes 4 mm. thick × 3–4 cm. long when mature; peduncle 5–10 mm. long; bracts round-subpeltate, glabrous in the center, marginally somewhat ciliate; fruit obpyramidal-trigonous, puberulous toward the top, stigmas 3, sessile.

Panama.

Panama: without location, *Seemann 1066.* colón: forests around Porto Bello, alt. 5–100 m., *Pittier 2477.*

59a. Piper septuplinervium var. **subpubinervium** Yuncker, var. nov.

Foliis 4.5–5 cm. latis, 12 cm. longis, luteo-glandulosis, venis supra puberulentis subtus glabratis; bracteis triangulari-subpeltatis, margine luteo-fimbriatis.

Leaves 4.5–5 cm. wide × 12 cm. long, yellow-glandular-dotted, nerves above puberulent, glabrous beneath; bracts triangular-subpeltate, marginally yellow-fringed.

Known only from the type locality.

Panama: without locality, 1859–1860, *Hayes 783* (no *678* also on the bottom of label) (Herb. New York Bot. Gard., type).

The glabrous, strongly nodose twigs, and glabrous, round-based leaves characterize this species which appears to be rather closely related to *P. aequale.*

60. Piper subquinquenerve Trel. in Field Mus. Nat. Hist. Bot. Ser. 18:363. 1937.

A shrub (?), nodose, essentially glabrous; flowering internodes slender and short; leaves lance-elliptic, apex acuminate, base subequilateral, acute, 2.5–3 cm. wide × 8–10 cm. long, pinnately nerved from the lower half, the nerves 3 on each side, long-ascending, connected with the midrib with cross-connecting nervules, commonly with two pair near the base and the third pair arising at about the middle, yellowish and microscopically puberulent glabrescent beneath, drying rather thin and dull, translucent; petiole 5–12 mm. long, grooved above but vaginate only at the very base; spikes as yet young, 2 mm. × 3.5 cm. long; peduncle about 1.5 cm. long; bracts round-subpeltate, smooth above; ovary and fruit not developed.

Known only from the following locality.

bocas del toro: Changuinola Valley, *Dunlap 452.*

61. PIPER INFRALUTEUM Trel. in Contr. U. S. Nat. Herb. 26:33. 1927.

A glabrous shrub; flowering internodes slender and short; leaves lance-elliptic or somewhat oblong, apex acuminate, base inequilateral with one side 2–3 mm. shorter, acute, 3–4 cm. wide × 10–12 cm. long, pinnately nerved from the lower half, the nerves slender, 4–5 on each side, with fine cross-connecting-anastomosing nervules, glandular-dotted on both sides, drying yellow beneath; petiole 5–7 plus 2–3 mm. long, vaginate at the base; spikes 2 mm. thick × 4–5 cm. long; peduncle about as long as the petioles; bracts round- or triangular-subpeltate, strongly yellow-fringed; ovary subglobose, smooth, stigmas slender, sessile.

Panama.

PANAMA: without locality, *Hayes 793*.

62. PIPER CRICAMOLENSE Trel. in Ann. Mo. Bot. Gard. 27:290. 1940.

A brittle, somewhat nodose shrub, 2–3 m. tall; flowering internodes short and relatively slender, microscopically strigulose especially about the nodes, quickly glabrescent; leaves elliptic or elliptic-obovate, apex abruptly sharp-acuminate, base subequilateral, obtuse, 4–7 cm. wide × 9–13 cm. long, pinnately nerved from below the middle, the nerves 4–5 on each side, strongly curved and unbranched upward, salient beneath, with conspicuous cross-connecting nervules, finely nervulose by transmitted light, glabrous on both sides or microscopically strigulose along the nerves, obscurely glandular-dotted beneath, drying papery, translucent; petiole scarcely 5 mm. long, microscopically strigulose, vaginate at the base only; spikes 2–3 mm. thick × 5–7 cm. long; peduncle 5 mm. long, rather stout, glabrous or microscopically strigulose; bracts triangular-subpeltate, marginally densely yellow-fringed; ovary narrowly ovoid-trigonous, yellow-glandular; stigmas 3, slender, sessile.

Known only from the following locality.

BOCAS DEL TORO: Río Cricamola, between Finca St. Louis and Konkintoë, alt. 10–50 m., *Woodson, Allen & Seibert 1927*.

The more or less microscopically strigulose twigs, low branching of the midrib, densely yellow-fringed bracts, and ovoid ovary characterize this species.

63. PIPER AEQUALE Vahl, Eclog. Amer. 1:4, *pl. 3*. 1796.

Schilleria aequalis Kunth, in Linnaea 13:687. 1839.
Artanthe aequalis Miq. Syst. Pip. 511. 1844.
?Piper Funckii C.DC. in DC. Prodr. 16[1]:310. 1869.
Piper substenocarpum C.DC. in Bull. Herb. Boiss. 6:492. 1898.
Piper concinnum C.DC. var. *trinitense* C.DC. in Urb. Symb. Ant. 3:304. 1902.
Piper Johnstoni C.DC. in Proc. Amer. Acad. 40:685. 1905.
Piper caledonianum C.DC. in Fedde. Rep. Sp. Nov. 15:1. 1917.
Piper aequale var. *substenocarpum* C.DC. in Ann. Conserv. & Jard. Bot. Genève 21:253. 1920.
Piper amphioxys Trel. in Contr. U. S. Nat. Herb. 26:31. 1927.
Piper ibaguense Trel. in Trab. Mus. Nac. Hist. & Jard. Bot. Madr. Ser. Bot. 33:50. 1936.
Piper zediogodiense Trel. ex Ll. Williams, Expl. Bot. Guyana Venezol. 177. 1942.

A glabrous, nodose shrub, 1–3 m. tall; flowering internodes slender and comparatively short; leaves elongated-elliptic, lance-elliptic or ovate, 3.5–9 × 12–17 cm. long, apex more or less attenuate, bluntly acuminate, base equilaterally acute or obtusish, pinnately nerved to the upper third or nearly throughout, the nerves mostly 4–5 or 6 on each side, with fainter intermediates and cross-connecting-anastomosing nervules, commonly 2 or 3 pairs approximated near the base and 1 or 2 pairs above the middle of the blade, the nerves often golden in dry specimens, drying rather firm, somewhat glossy, narrowly revolute, translucent; petiole about 5–10 mm. long or sometimes up to 1.5 cm. on lower leaves, commonly vaginate near the base but occasional leaves vaginate to the middle or above; spikes 2–4 mm. thick and up to 10 cm. long; peduncle commonly about as long as the petiole; bracts rounded dome-shaped when young with submarginal fringe, becoming round- or triangular-subpeltate and loosely fringed; fruit small, obpyramidal-trigonous, convex at the top, glabrous; stigmas slender, sessile.

West Indies, northern South America, and Panama.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 495*. COLÓN: Loma de la Gloria, near Fató (Nombre de Dios), alt. 10–104 m., *Pittier 4239*.

63a. PIPER AEQUALE var. **laurifolium** (Trel.) Yuncker, comb. nov.

Piper amphioxys Trel. var. *laurifolium* Trel. in Contr. U. S. Nat. Herb. 26:31. 1927.

The nerves beneath very minutely hirtellous; the leaves mostly with 3 strongly ascending nerves on each side with two from near the base and the third from near or above the middle.

Known only from the type locality.

DARIÉN: foothills of Garagará, Sambú basin, alt. 300–500 m., *Pittier 5598* (U. S. Nat. Herb., TYPE).

This species appears to be widely distributed in tropical America. The Panamanian specimens here cited agree in all respects with those from South America and the West Indies believed to represent this species.

64. PIPER SAMBUANUM C.DC. in Smiths. Misc. Coll. 71[6]:13. 1920.

A shrub (?), nodose, glabrous; flowering internodes slender and short, obscurely granular and glandular-dotted; leaves lance-elliptic to obliquely lanceolate, apex acuminate, base inequilateral with one side about 2 mm. shorter, obtuse or the longer side subcordulate, 5–6.5 cm. wide × 13–17 cm. long, pinnately nerved from below the upper third, the nerves about 4 on each side, or 5 with the lowermost obscure, with rather strong cross-connecting-anastomosing nervules, glandular-dotted, drying papery, translucent, pellucid-dotted; petiole about 3 plus 2 mm. long, stout, vaginate-winged to the lower blade margin; spikes 2 mm. thick × 8–10 cm. long; peduncle scarcely 1 cm. long, stoutish; bracts small, round- or triangular-subpeltate, marginally ciliolate; ovary glabrous; stigmas sessile; fruit not developed.

Known only from Sambú basin, Darién.

DARIÉN: foothills of Garagará, Sambú basin, alt. 30–500 m., *Pittier 5663, 5726*.

The glabrous, glandular-dotted, nodose twigs, short-petioled leaves, and slender spikes characterize this species.

65. PIPER TECUMENSE Trel. in Contr. U. S. Nat. Herb. 26:29. 1927.

A shrub, scarcely 2 m. tall, essentially glabrous; flowering internodes slender and elongating downward, glabrous or very slightly evanescently crisp-pubescent, slightly pubescent at the nodes; leaves elliptic, elliptic-ovate, or lance-ovate, apex gradually sharp-acuminate, base nearly equilateral, rounded, one side commonly about 2 mm. shorter, pinnately nerved from the lower half, the nerves about 4 on each side, submarginally loop-connected, with cross-connecting-anastomosing nervules, not glandular-dotted, 4–5.5 cm. wide × 10–14 cm. long, glabrous above, the nerves beneath obscurely and minutely appressed-pubescent or glabrescent; petiole scarcely 5 plus 2 mm. long, vaginate at the base; stipules and stipular line slightly pubescent; spikes as yet young, 1.5 mm. thick × 3.5 cm. long; peduncle slender, 1 cm. long, glabrous; bracts rounded-subpeltate, yellow-fringed; ovary and fruit not developed.

Known only from the following locality.

PANAMÁ: Río Tecumen, *Standley 29358.*

66. PIPER CRASSISPICATUM Opiz in Presl, Reliq. Haenk. 1:152. 1830.

Artanthe crassispicata Miq. Syst. Pip. 521. 1844.

A shrub (?), nodose, glabrous; leaves elliptic- or oblong-ovate, apex rather abruptly acuminate, base equilaterally subacute, 10–13 cm. wide × 20–22 cm. long, pinnately nerved from below the upper fourth, the nerves about 7 on each side, drying subcoriaceous; petiole 1.5–2 cm. long, vaginate-winged downward; spikes 4 mm. thick × 5–6.5 cm. long; peduncle about 5 mm. long; bracts triangular-subpeltate, ciliate; fruit said to be obpyramidal-triquetous and stigmas sessile.

Known only from the type specimen in the Prague herbarium collected by Haenke.

An obscure species apparently distinguished by the rather large leaves and number of nerves. The type has not been seen. The description is based on notes of the type made by the late Professor Trelease from the specimen at Prague.

67. PIPER BOGOTENSE C.DC. in Jour. Bot. 4:214. 1866.

?Piper fistulosum C.DC. loc. cit. 212. 1866.
Piper fuscesens C.DC. in DC. Prodr. 16[1]:291. 1869, not *Artanthe fuscescens* Miq.
Piper durirameum C.DC. in Bull. Herb. Boiss. 6:484. 1898.
Piper tungurahuae Sodiro, Contr. Conoc. Fl. Ecuator. Monogr. 1, 2nd ed. Nuev. Adic. 1, [1902.]
Piper oblitum Trel. in Contr. U. S. Nat. Herb. 26:22. 1927.
Piper bogotense C.DC. var. *usaquemanense* Trel. in Trab. Mus. Nac. Hist. & Jard. Bot. Madr. Ser. Bot. 33:48. 1936.
Piper usaquemense (Trel) Peréz Arbeláez, Pl. Utiles de Col. 207, *f. 245.* 1947.

A shrub or small tree, up to 8 or 10 m. tall; flowering internodes comparatively short, sparsely pubescent or glabrate; leaves ovate, mostly 6–8 or 9 cm. wide × 10–15 cm. long, or infrequently up to 15–18 × 20 cm., apex acuminate, or sometimes rather blunt, base more or less inequilateral with one side often shorter, rounded, obtuse, cordate, or acute, pinnately nerved from the lower third, the major nerves 3 or 4 or in larger leaves 5 on each side, with reduced nerves upward, more or less pubescent above at least along the nerves, often somewhat glossy when dry, from densely crisp-pubescent to subglabrate beneath, but with the nerves mostly persistently rather densely crisp-pubescent, the hairs more abundant on the sides of the nerves, mostly densely ciliolate, glandular-dotted, drying rather dark, firm, translucent; petiole 1–1.5 or 2 cm. long, or on lower leaves up to 5 cm., mostly densely crisp-pubescent-tomentose, vaginate at the base; spikes 5–7 mm. thick and up to 8 cm. long but mostly somewhat shorter; peduncle about 10 mm. long, thinly crisp-pubescent glabrescent; bracts round- or triangular-subpeltate, marginally fringed; fruit obovoid, stigmas 3–4, lanceolate, recurved, sessile.

Northern South America and Panama.

Panama: without location, *Hayes 803*.

It has been impossible to find any differences between this specimen from Panama and those believed to represent *P. bogotense* from South America.

68. Piper sperdinum C.DC. in Smiths. Misc. Coll. 71[6]:1. 1920.

A low shrub; flowering internodes relatively short, densely villous with a mixture of scattered hairs up to 2 mm. or more long; leaves inequilaterally elliptic or subovate, the midrib much nearer one side, apex sharp and long-acuminate, base strongly inequilateral with one side 1–3 mm. shorter at the petiole and rounded-cordulate, the longer side auriculate, the lobe 1–2 cm. long and covering the petiole, 6–9 or 10 cm. wide × 15–24 cm. long, pinnately nerved from below the middle, the nerves mostly 4–5 on each side, prominent beneath and with rather prominent cross-connecting-anastomosing nervules, submarginally loop-connected, glabrous above except for a few hairs on the midrib near the base, pubescent beneath with the nerves densely so with an intermixture of spreading long hairs, margin not ciliate, obscurely glandular-dotted, drying rather papery, translucent; petiole about 3–5 plus 1–3 mm. long, densely hairy, vaginate at the base; spikes about 3 mm. thick × 6–7 cm. long, with a slender, bearded, aristate tip up to 1 cm. long; peduncle up to 2 cm. long, densely pubescent; bracts truncately triangular-subpeltate, with usually 2–4 rather prominent dorsal setae, or glabrous, the pedicel margins setose; rachis ridges fimbriate; fruit obpyriform-trigonous, granular-papillate, stigmas slender, sessile.

Near Puerto Obaldía, San Blas Coast.

San Blas: hills back of Puerto Obaldía, alt. 50–200 m., *Pittier 4301, 4348*.

A very well-marked species with its dimorphic pubescence, auriculate leaves, and papillate fruit.

69. PIPER **perbrevicaule** Yuncker, sp. nov.

Suffrutex, ca. 15 cm. altus, caudice conferte villoso, pilis 1–2 mm. longis; foliis rhombico-elliptico-obovatis, apice abrupte breviter acuminatis, basi inaequaliter subcordato-auriculatis, lobo longiore petiolum obtegente, utrinque longe villosis, pilis 1 mm. vel ultra longis, subtus ad venas patentibus, a medio infero pinnatim venosis, venis 4 + 5–6; petiolo haud 1 cm. longo, dense longe villoso, sub base vaginato; spicis 1–2 mm. crassis, 3 cm. longis; pedunculo 3–5 cm. longo, dissite villoso; bracteis triangulari-subpeltatis, glabratis; drupa ovoideo-subglobosa subacuminata; stigmatibus gracilibus sessilibus.

A very small subshrub, 15 cm. or less tall; stem drying somewhat ridged, densely villous, the hairs 1 mm. or more long; internodes mostly 1–2 cm. long; leaves somewhat pustular above, obliquely elliptic-obovate-rhomboidal, the midrib much nearer one side, 2.5–4 cm. wide × 7–9 cm. long, apex abruptly short-acuminate, base subequal at the petiole, the shorter side obtuse or cordulate, the longer side auriculate with the lobe, about 1 cm. long and covering the petiole, long-villous on both sides, the nerves beneath more strongly so with the hairs essentially erect and 1 mm. or more long, pinnately nerved from the lower half, the nerves 4 + 5–6 with cross-connecting-anastomosing nervules, drying rather thin, green, translucent; petiole scant 1 cm. long, densely long-villous, vaginate toward the base; spikes red, purple, or olive-green when fresh, 1–2 mm. thick × 3 cm. long; peduncle 3–5 cm. long, slender, sparsely villous glabrescent; bracts triangular-subpeltate, glabrous; fruit very small, ovoid-subglobose with pointed apex, glabrous; stigmas slender, sessile.

Fig. 9. *Piper perbrevicaule*

Known only from the type locality.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, Water Valley, Oct. 1, 1940, *von Wedel 971* (Herb. Missouri Bot. Gard., TYPE); Nov. 1, 1940, *von Wedel 1469*.

69a. PIPER PERBREVICAULE var. **subglabrilimbum** Yuncker, var. nov.

Foliis supra glabratis, subtus ad venas haud conferte villosis, pilis haud 1 mm. longis.

Leaves 4.5 cm. wide × 8–9 cm. long, upper surface of blade glabrous, the nerves beneath thinly villous, the hairs less than 1 mm. long.

Known only from the type locality.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, Oct. 8, 1940, *von Wedel 1074* (Herb. Missouri Bot. Gard., TYPE).

The very small plants, long-villous stems, and strongly auriculate leaves are distinctive characteristics of this species.

70. Piper leptocladum C.DC. in Anal. Inst. Fis.-Geogr. Costa Rica 9:164. 1897.

Piper dilatatum Rich. var. *leptocladum* C.DC. in Candollea 1:96. 1923.
Piper diazanum Trel. in Contr. U. S. Nat. Herb. 26:34. 1927.
Piper diazanum var. *viae-kobeanae* Trel. in Ann. Mo. Bot. Gard. 27:290. 1940.
Piper tabernillanum Trel. loc. cit. 298. 1940.

A shrub, up to about 3 m. tall; flowering internodes slender and rather short, sparsely crisp-hairy; leaves subrhombically elliptic, lanceolate, or subovate, smooth or slightly rugose, occasionally slightly scabrous, apex gradually sharp-acuminate, base rounded, obtuse to cordulate, or subcordate, equal at the petiole or with one side slightly shorter, 4–5 or sometimes 7 cm. wide × 10–17 cm. long, pinnately nerved from the lower half, the nerves 4–5 on each side, puberulent above along the nerves, rather sparsely appressed- or crisp-pubescent on the nerves beneath, glandular-dotted, drying rather thin, green, translucent; petiole 5–10 mm. long, crisp-villous, vaginate at the base; spikes 3 mm. thick × 6–9 cm. long; peduncle about 5 mm. long, pubescent or glabrate; bracts triangular-subpeltate, yellow-fringed; fruit obpyramidal-trigonous, glabrous, green to dark-colored, stigmas small, sessile.

Panama and Costa Rica.

CANAL ZONE: vicinity of Fort Sherman, *Standley 30953, 30974, 30996;* Monte Lirio, *Maxon 6843;* Matachín to Las Cascadas, *Cowell 338;* Las Cascadas Plantation, near Summit, *Standley 25798, 29625;* Fort San Lorenzo, Fort Sherman Military Reservation, *Maxon & Valentine 7012*—the leaves on this specimen are smaller and less pubescent than customary for this species but it appears to agree in all other characters; Barro Colorado Island, *Bailey & Bailey 55, 104, 242; Kenoyer 307, 308; Standley 40862, 41035;* Cerro Gordo, near Culebra, *Standley 26006;* around Tabernilla, along the railroad, alt. 20–25 m., *Pittier 3828;* Empire, *Miller 1765;* Mt. Hope Cemetery, *Standley 28802;* Obispo, *Standley 31671;* Fort Kobe road, *Woodson, Allen & Seibert 1412.* COLÓN: forests around Porto Bello, alt. 5–100 m., *Pittier 2428.* PANAMÁ: Juan Díaz, deep woods, *Killip 3114.*

Fig. 10. *Piper dimorphotrichum*

This species rather closely resembles *P. dilatatum* of South America but differs because of its glabrous fruit and other minor characters.

71. Piper **dimorphotrichum** Yuncker, sp. nov.

Frutex, 3 m. altus, internodiis floriferis sat brevibus crassisque, conferte subretrorse brunneo-hirsutis, pilis brevibus longisque intermixtis, pilis longis ad 3–4 mm. vel. ultra longis; foliis late ellipticis, apice attenuatim acuminatis, basi oblique cordulatis vel subauriculatis, lobis subaequalibus vel lobo longiore petiolum fere aequante, a medio infero pinnatim venosis, venis utrinque 5–8, trabibus gracilibus anastomosantibus, supra sparse villosis, subtus pubescentibus (confertius ad venas), pilis erectis, heteromorphis, brevioribus longioribusque intermixtis; petiolo vix 1 mm. longo, a medio deorsum vaginato;

spicis 5 mm. crassis, 5–6 cm. longis; pedunculo gracili, 4–6 cm. longo, villoso; bracteis triangulari-subpeltatis, margine fimbriatis; drupa oblonga lateraliter compressa, glabrata, glandulosa, stigmatibus sessilibus.

A shrub, up to 3 m. tall; flowering internodes rather short and slender, densely subretrorsely brown-hairy, the hairs of different lengths up to about 1 mm. with intermixed scattered long-spreading hairs up to 3–4 mm. or more; leaves broadly elliptic, apex attenuately acuminate, base obliquely cordulate or subauriculate, subequal at the petiole, the lobes subequal or one larger and about as long as the petiole, 5–10 cm. wide × 15–20 cm. long, pinnately nerved from below the middle, the nerves 5–8 on each side, approximated downward, with prominent, slender, cross-connecting-anastomosing nervules, sparsely villous above, staring pubescent beneath, the nerves more densely so, interspersed with scattered long hairs, drying thin, brown, translucent; petiole scarcely 1 cm. long, densely villous with mixed long hairs, vaginate below the middle; spikes 5 mm. thick × 5–6 cm. long when mature, with a slender, seta-like apex up to 7 mm. long; peduncle 4–6 cm. long, villous with an intermixture of long hairs; bracts triangular-subpeltate, marginally fringed with rigid hairs, those on the dorsal margin somewhat longer; drupe compressed-oblong, glabrous, glandular, stigmas slender, sessile.

Known only from the type locality.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1015;* Water Valley, *von Wedel 1446*—this specimen is not as densely pubescent as the others; Nov. 9, 1940, *von Wedel 1569* (Herb. Missouri Bot. Gard., TYPE).

The wide difference in the length of the hairs, rather large, subauriculate leaves, setose spikes, and long slender peduncles are distinctive characters of this species.

72. PIPER PSEUDO-GARAGARANUM Trel. in Contr. U. S. Nat. Herb. 26:28. 1927.

Shrub, 1–2 m. tall, nodose; flowering internodes short and slender, moderately to sparsely villous, glabrescent downward, hairs up to 1 mm. or more long, somewhat granular and glandular-dotted; leaves elliptic or elliptic-lanceolate, apex rather long-acuminate, base rounded, inequilateral, one side 2–4 mm. shorter, obtuse, the longer side cordulate, pinnately nerved from the lower half, the nerves mostly alternate, 4 or in larger leaves 5 on each side, with slender cross-connecting and anastomosing nervules, 4.5–7.5 cm. wide × 14–20 cm. long, smooth or very slightly scabrous, sparsely long-villous above, loosely long-villous beneath, at least along the nerves, the hairs mostly erect, drying papery, glandular-dotted, translucent; petiole 2–4 plus 2 mm. long, villous, vaginate at the base; spikes 3 mm. thick × 7.5 cm. long; peduncle scarcely 1 cm. long, granular, glabrous; bracts round-subpeltate, moderately fringed, a few dorsal hairs longer; fruit obpyramidal-trigonous, glandular-dotted, apex truncate, glabrous, stigmas sessile.

Panama.

CANAL ZONE: Barro Colorado Island, *Standley 31409, 41164.* DARIÉN: Caña-Cuasi Trail (Camp 2), Chepigana Distr., alt. 600 m., *Terry & Terry 1427.*

The specimens cited differ considerably in the size of the leaves. Those on *No. 41164* are scarcely 5 cm. wide × 14–15 cm. long while those on *No. 1427* are 7–8 cm. wide × 18–20 cm. long. *No. 31409* is intermediate in size. The description of the spike characters are from *Terry & Terry 1427*. The spikes on the other two specimens are very young and do not exhibit ovary or fruit characters. All specimens agree otherwise.

73. PIPER CATIVALENSE Trel. in Contr. U. S. Nat. Herb. 26:34. 1927.

Shrub, 2–3 m. tall; flowering internodes slender, rather elongate, villous; leaves elliptic to subobovate, apex rather abruptly acuminate, base inequilateral, cordulate, one side slightly shorter, 6–7 cm. wide × 12–14 cm. long, pinnately nerved from the lower half or two-thirds, the nerves mostly 5 on each side, with cross-connecting and anastomosing nervules, somewhat glossy green, very slightly scabrous and sparsely villous above, the nerves scarcely hairy, villous beneath, especially along the nerves, marginally somewhat ciliate, glandular-dotted on both sides, drying thin, translucent; petiole 5–10 plus 2 mm. long, villous, vaginate toward the base; inflorescence not known.

Known only from the following locality.

COLÓN: between France Field, Canal Zone, and Cativa1, *Standley 30206*.

The absence of inflorescence leaves the position of this species somewhat questionable.

74. PIPER PSEUDO-LANCEAEFOLIUM Trel. in Contr. U. S. Nat. Herb. 26:170. 1929.

Piper liratinerve Trel. in Ann. Mo. Bot. Gard. 24:186. 1937.

A shrub, 2 m. or more tall; upper internodes slender, sparsely to densely appressed-villous; leaves subinequilaterally lanceolate, apex gradually sharply long-acuminate, base inequilateral with one side about 2 mm. shorter, obtuse, cordulate, or sometimes acutish, mostly 4–5 cm. wide × 14–17 cm. long, pinnately nerved from the lower half, the nerves mostly 7–8 on each side, impressed above, salient beneath, veiny, rugescent and subappressed-pubescent above, scarcely lacunose beneath, appressed-pubescent, the nerves densely so, obscurely pale glandular-dotted, drying firm, translucent; petiole about 5 plus 2 mm. long, vaginate-winged to near the blade, villous; spikes 2–3 mm. thick × 8–12 cm. or more long, apiculate, curved; peduncle up to 2–3 cm. long, pubescent; bracts triangular-subpeltate, densely yellow-fringed; fruit obpyramidal-trigonous, dark, apex truncate, glabrous, stigmas slender, sessile.

Costa Rica and Panama.

PANAMÁ: without locality, *Née 350, 400*. CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, alt. 1300–1900 m., *Seibert 158*; vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., *Woodson, Allen & Seibert 910*.

This species resembles *P. lanceaefolium* in most characters and may be too close to it, but it differs because of its less but more coarsely rugose leaves which are scarcely lacunose beneath, and with the base much less cordulate-auriculate.

75. PIPER LINEARIFOLIUM C.DC. in Linnaea 37:355. 1872.

Piper alveatum Trel. in Ann. Mo. Bot. Gard. 27:287. 1940.
Piper arctilimbum Trel. loc. cit. 288. 1940.
Piper arctilimbum var. *Alleni* Trel. loc. cit. 1940.

A low, bushy shrub, scarcely 2 m. tall; flowering internodes moderately slender and short, gray-pubescent; leaves lanceolate, apex gradually long- and sharp-acuminate, base inequilateral with one side 2–3 mm. shorter, obtuse, cordulate, or some leaves acute, mostly 2–3.5 cm. wide × 10–17 cm. long, subrugescent in age, pinnately nerved from the lower third, the nerves 4–5 or occasionally 6 on each side, prominent beneath, somewhat impressed above, subequally spaced, subparallel and sharply ascending from the midrib, appressed-silky-pubescent on both sides, the nerves more densely so beneath, glandular-dotted, drying rather firm, translucent, pellucid-dotted; petiole 3–5 plus 2–3 mm. long, pubescent, vaginate to near the blade; spikes 2–3 mm. thick × 5–9 cm. long, generally curved; peduncle 5–15 mm. long, pubescent; bracts triangular-subpeltate, densely yellow-fringed; fruit obpyramidal, 3- or 4-sided, glabrous; stigmas small, sessile.

Costa Rica and Panama.

BOCAS DEL TORO: vicinity of Nievecita, alt. 0–150 m., *Woodson, Allen & Seibert 1837;* Chiriquí Trail, *von Wedel 2176.* CHIRIQUÍ: vicinity of El Boquete, alt. 1000–1300 m., *Maxon 5140; Killip 3638;* Isla de Coiba, *Mendez 122;* rocky plains about 5 miles south of Boquete, alt. 900 m., *Allen 4705.* COCLÉ: El Valle, *Miller 1813;* vicinity of El Valle de Antón, alt. 600 m., *Allen 2003;* Penonomé and vicinity, alt. 15–300 m., *Williams 54.* COLÓN: along Río Fató, alt. 10–100 m., *Pittier 3881.*

The narrowly lanceolate, silky-pubescent leaves, with sharply ascending nerves, curved spikes, and yellow-fringed bracts distinguish this species.

76. PIPER PANAMENSE C.DC. in Jour. Bot. 4:216. 1866.

Piper citrifolium Lam. var. *panamense* C.DC. in Candollea 1:114. 1923.

A shrub; flowering branches short, nodose, rather slender, densely subretrorsely crisp-pubescent laterally below the petioles, glabrescent downward, glandular-papillate; leaves elliptic-ovate, apex acute to short-acuminate, base with one side slightly shorter at the petiole, rounded, obtuse, or one or both sides acutish, pinnately nerved below the upper third, the nerves 4–5 on each side, with cross-connecting-anastomosing nervules, 5–7 cm. wide × 10–15 cm. long, glabrous above, puberulent beneath, at least along the nerves, glandular-dotted, drying firm and somewhat glossy, translucent; petiole scarcely 1 cm. long, rather densely subretrorsely pubescent, vaginate near the base; spikes 3 mm. thick × 4–5 cm. long; peduncle about 5 mm. long, puberulent; bracts triangular-subpeltate, ciliate; fruit oblong, compressed, apex truncate, depressed about the stigmas, strongly papillate-puberulent; stigmas sessile.

Panama.

BOCAS DEL TORO: Laguna de Chiriquí and vicinity, *Hart 124.* CANAL ZONE: Chagres, *Fendler 270.*

The densely papillate fruit and comparatively short, stout spikes distinguish this species.

77. PIPER CALLIBRACTEUM C.DC. in Smiths. Misc. Coll. 71[6]:13. 1920.

Piper chamissonis (Miq.) Steud. var. *rubellibracteum* C.DC. loc. cit. 1920.
Piper subnudibracteum C.DC. loc. cit. 14. 1920.
Piper nitidifolium C.DC. loc. cit. 1920.

A shrub, 1.5–3 m. tall; flowering internodes rather slender and short, glabrate, pale-dotted; leaves elliptic-lanceolate or subovate, apex acuminate, base inequilateral with one side mostly slightly shorter, acute on both sides or one side obtusish, 5–8 cm. wide × 13–22 cm. long, smooth or slightly rugose, pinnately nerved from the lower half, the nerves 4 or sometimes 5 on each side, with cross-connecting and anastomosing nervules, glabrous above, obscurely appressed-pubescent beneath, at least on the smaller nerves, drying green, slightly paler and pale-glandular-dotted beneath; petioles up to 3 cm. long, glabrous, vaginate toward the base; spikes 3 mm. thick × 8–10 cm. long, short-mucronate; peduncles 1–1.5 cm. long, glabrous; bracts rather small, triangular-lunate-subpeltate, somewhat umbonate, sparsely short-fringed; fruit compressed, white-papillate-puberulent at the top, stigmas sessile.

Western Panama.

CHIRIQUÍ: forests around El Boquete, alt. 1000–1300 m., *Pittier 2940; Maxon 4943; Pittier 2898, 2899;* between Cerro Vaca and Hato del Loro, alt. 850–1100 m., *Pittier 5390.*

The petioles of the type of *P. submudibracteum* are scarcely 1 cm. long and the leaves are slightly more pubescent along the nerves beneath than are the types of the other species included here. All agree, however, in the pubescent ovary and fruit, small, scarcely fringed bracts, and other characters to such a degree that it is believed they all represent a single species which usually has petioles 1–3 cm. long, and nerves scarcely pubescent beneath.

78. PIPER **Wedelii** Yuncker, sp. nov.

Frutex, 1–2 m. altus; internodiis floriferis gracilibus brevibusque, delicate costulatis, dissite hirtulis; foliis subrhombico-ellipticis, apice longius acute acuminatis, basi oblique, latere altero obtuso, ad petiolum 3 mm. breviore, caetero rotundato cordulato, a medio deorsum pinnatim venosis, venis utrinque 5–6, supra glabratis vel dissite scabridis, subtus ad venas sat dissite substrigosis; petiolo ca. 5 cum 3 mm. longo, ad basem vaginato; spicis immaturis, 2 mm. crassis, 6 cm. longis, mucronatis; bracteis triangulari-subpeltatis, glabratis, dorso papilloso-callosis; drupa ignota.

A tree-like shrub, 1–2 m. tall; flowering internodes short and slender, finely ridged when dry, granular-roughened, young growth obscurely hirtellous; leaves

subrhomboidal-elliptic, apex sharply long-acuminate, base oblique, one side 3 mm. shorter at the petiole and obtuse, the longer side rounded, cordulate, 9–10 cm. wide × 20–22 cm. long, pinnately nerved from the lower half, the nerves 5–6 on each side with slender cross-connecting-anastomosing nervules, glabrous or slightly scabrous above, the nerves beneath rather sparsely substrigose, glandular-dotted on both sides, drying thin, translucent; petiole about 5 plus 3 mm. long, vaginate at the base; spikes as yet young, red when fresh, 2 mm. thick × 6 cm. long, mucronate; bracts triangular-subpeltate, glabrous, with a dorsal papillate callus; ovary and fruit not present.

Known only from the type locality.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, Oct. 2, 1940, *von Wedel 1021* (Herb. Missouri Bot. Gard., TYPE).

78a. PIPER WEDELII var. **retrohirsutum** Yuncker, var. nov.

Internodiis floriferis retrorse hirsutis; foliis ellipticis, 4–5 cm. latis, 11–13 cm. longis, supra scabridis obscure hispidulisque, subtus ad venas strigosis, glanduloso-punctatis.

Flowering internodes retrorsely hirsute; leaves elliptic, 4–5 cm. wide × 11–13 cm. long, obscurely hispidulous and scrabous above, the nerves beneath strigose, glandular-dotted.

Known only from the type locality.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, Water Valley, Nov. 9, 1940, *von Wedel 1575* (Herb. Missouri Bot. Gard., TYPE).

This species resembles *P. erubescentispicum* in the appearance of the spikes but it differs because of its larger, non-villous, conspicuously glandular, and scarcely scabrous leaves. The dorsally calloused floral bracts are rather distinctive. The smaller leaves and strongly retrorsely hirsute twigs contrast the variety.

79. PIPER VERRUCULAEPETIOLUM Trel. in Field Mus. Publ. Bot. 18:368. 1937.

Shrub, nodose; flowering internodes comparatively short and slender, glabrous, pale granular-dotted; leaves obliquely ovate-elliptic, apex short-acuminate, base obliquely inequilateral, one side 2–3 mm. shorter, the longer side strongly cordulate, 7–10 cm. wide × 17–24 cm. long, pinnately nerved below the upper third, the nerves 6–8 on each side, with cross-connecting and anastomosing nervules, glabrous above, very finely puberulent on the nerves beneath, yellow glandular-dotted on both sides, drying thin, translucent; petiole 7 plus 2–3 mm. long, strongly granular, glabrous or sparingly puberulent, vaginate at the base; spikes 3 mm. thick × 7–8 cm. long; peduncle about 5 mm. long, glabrous, granular; bracts triangular-sub-peltate, marginally yellow-fringed; fruit trigonous, glabrous, glandular-dotted, truncate; stigmas sessile.

Known only from the following locality.

BOCAS DEL TORO: Farm Six, Changuinola Valley, *Dunlap 494.*

80. Piper hirtellipetiolum C.DC. in Smiths. Misc. Coll. 71[6]:3. 1920.

A conical, tree-like shrub, 1.5–2 m. tall, nodose; flowering internodes very short and slender, glandular-dotted, glabrous or at first with a few scattered hairs; leaves lanceolate, apex gradually acuminate, base subinequilateral, one side 1–2 mm. shorter, acute or obtusish, 2.5–3.5 cm. wide × 9–13 cm. long, pinnately nerved from below the middle, the nerves 3–4 on each side, loop-connected upward, with cross-connecting and anastomosing nervules, glabrous on both sides or the midrib sparsely hairy near the base, drying light green, glossy above, pale glandular-dotted beneath; petiole scarcely 5 plus 2 mm. long, loosely villous, vaginate at the base; spikes 3 mm. thick × 4–5 cm. long; peduncle 5 mm. long, puberulent above the middle; bracts triangular-subpeltate, copiously yellow-fringed, usually annular, alternating with the dark fruits; fruit rounded-obovoid (?), glabrous, black; stigmas small, sessile.

Known only from David, Chiriquí.

chiriquí: vicinity of David, alt. 30–80 m., *Pittier 2832*.

80a. Piper hirtellipetiolum var. **tapianum** (Trel.) Yuncker, comb. nov.

Piper tapianum Trel. in Contr. U. S. Nat. Herb. 26:30. 1927.

Shrub, 3 m. tall; twigs moderately to rather densely crisp-villous; leaves 3.5–6.5 cm. wide × 10–16 cm. long, glabrous and glossy above, strongly glandular-dotted beneath with the nerves crisp-pubescent; petioles crisp-hairy; spikes 5–6 cm. long.

Central Panama.

panamá: near Tapia River, Juan Díaz region, June 1–3, 1923, *Maxon & Harvey 6700* (U. S. Nat. Herb., type); Río Tapia, *Standley 26122;* Perlas Archipelago, San José Island, *Johnston 1360; Erlanson 176.*

80b. Piper hirtellipetiolum var. **Harveyanum** (Trel.) Yuncker, comb. nov.

Piper subtrinerve var. *Harveyanum* Trel. loc. cit. 30. 1927.

Piper subtrinerve Trel. in Contr. U. S. Nat. Herb. 26:29. 1927.

Piper perfugii Trel. in Ann. Mo. Bot. Gard. 27:295. 1940.

An essentially glabrous, somewhat nodose shrub, 1.5–3 m. tall; leaves lance-elliptic, 2–4.5 cm. wide × 7–15 cm. long, glabrous or rarely with a few scattered short hairs on the nerves beneath; petiole glabrous; spikes 3–4 mm. thick × 4–6 cm. long; peduncle with a few short hairs near the spike.

Fig. 11. *Piper hirtellipetiolum* var. *Harveyanum*

Panama.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 231*—the spikes of this specimen are apiculate. CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., *Woodson, Allen & Seibert 928*—this specimen has leaves somewhat smaller than usual. COCLÉ: El Valle, *Miller 1814*. CANAL ZONE: Las Sabanas, *Bro. Celestine 110;* foot of Corozal Hill, *Miller 1790*. PANAMÁ: near Tapia River, Juan Díaz region, *Maxon & Harvey 6684, 6734;* Juan Díaz, *Standley 30600;* along the Corozal Road, near Panamá, *Standley 26854;* Tumba Muerto Road, near Panamá, *Standley 29710;* Punta Paitilla, *Piper 5410;* east of Río Tecumen, *Standley 26563;* between Las Sabanas and Matías Hernández, *Standley 31836;* Taboga Island, *Standley 27869; Pittier 3618* (U. S. Nat. Herb., TYPE); Perlas Archipelago, San José Island, *Johnston 81, 754*.

The specimens included under this species, including the varieties, all agree to such a degree that it does not appear advisable to maintain the varieties as separate species. The chief distinction appears to be in the character and amount of pubescence.

81. PIPER SUBCAUDATUM Trel. in Contr. U. S. Nat. Herb. 26:31. 1927.

Shrub (?), nodose; flowering internodes slender and short, somewhat ridged and striate-pilose, especially below the petioles; leaves obliquely elliptic or elliptic-obovate, apex abruptly subcaudately long-acuminate, tip about 2.5 cm. long, base narrowed downward, obtuse or subcordulate, one side about 3 mm. shorter, 6–8 cm. wide × 13–16 cm. long, pinnately nerved below the upper third, the nerves 5 or 6 on each side, with cross-connecting-anastomosing nervules, submarginally loop-connected upward and, excepting the innermost pair, not continuing to the apex, glabrous above, the nerves beneath appressed-puberulent, both sides glandular-dotted, drying somewhat glossy, thin, translucent; petiole about 5 plus 3 mm. long, hairy-lined beneath, vaginate near the base; spikes as yet very young, 1 mm. thick × 1 cm. long; peduncle sparsely hairy; bracts rounded-subpeltate, marginally ciliate; ovary and fruit not developed.

Known only from Sambú basin, Darién.

DARIÉN: foothills of Garagará, Sambú basin, alt. 30–500 m., *Pittier 5612*.

81a. PIPER SUBCAUDATUM var. **maternale** (Trel.) Yuncker, comb. nov.

Piper maternale Trel. in Field Mus. Publ. Bot. 18:349. 1937.

Leaves somewhat oblique, elliptic or elliptic-subovate, apex tip about 1 cm. long, base more strongly cordulate.

Panama.

BOCAS DEL TORO: vicinity of Almirante, *Cooper 189, 210* (Herb. New York Bot. Gard. and Herb. Univ. Ill., ISOTYPES); Changuinola Valley, Bar Mouth, *Dunlap 536;* Old Bank Island, *von Wedel 2047*.

The shape and venation of the mostly cordulate-based leaves characterize this species. It is to be distinguished from *P. culebranum* chiefly because the lateral

nerves do not continue toward the apex as in that species. There is some question whether var. *maternale* differs sufficiently from the species to merit recognition. The leaf shape and shorter apex are the main differential features.

82. PIPER GONOCARPUM Trel. in Contr. U. S. Nat. Herb. 26:28. 1927.

A shrub, 2 m. tall; flowering internodes moderately slender and elongate, densely retrorsely dingy-pubescent; leaves lance-elliptic or suboblong, apex gradually acuminate, base somewhat inequilateral, rounded or cordulate, one side slightly shorter, 5–6.5 cm. wide × 15–17 cm. long, pinnately nerved from below the upper third, the nerves about 6 on each side, glabrous above, the midrib impressed below the middle, hirsute beneath, the nerves rather densely so, the hairs staring, drying rather thick, subtranslucent, glossy above, narrowly revolute; petiole about 10 plus 2 mm. long, densely pubescent, vaginate to the blade; spikes 7–8 mm. thick × 4 cm. long, caudate at the tip; peduncle scarcely 1 cm. long, sparsely hairy; bracts broad, narrowly lunate-concave, glabrous; fruit depressed-quadrangular, 2–3 mm. in diameter, ridged, granular, glabrous; stigmas 2, broad, sessile.

Canal Zone.

CANAL ZONE: hills north of Frijoles, *Standley 27437*.

The short, thick spikes, and large, angular fruits are distinctive of this species.

V. KEY TO SPECIES WITH LEAVES PINNATELY NERVED TO THE UPPER FOURTH OR THROUGHOUT.

a. Midrib branches 10–15 on each side, subequally spaced; leaves mostly 10 cm. or more wide; spikes mostly 8–10 mm. thick ..... 83. P. AUGUSTUM
aa. Midrib branches usually less than 10 and commonly variously spaced; leaves mostly narrower.
b. Leaf base strongly inequilateral with one side mostly 5–10 mm. shorter at the petiole.
c. Leaves somewhat scabrid; stems villous; petiole vaginate to the middle ..... 84. P. STEVENSI
cc. Leaves not scabrid; stems glabrous or puberulent; petiole vaginate-winged to the blade, the wings often protracted at the blade.
d. Leaves 25 cm. or more long; nerves 6–7 on each side ..... 85. P. COLONENSE
dd. Leaves mostly less than 20 cm. long; nerves 8–10 on each side.
e. Leaf apex very short and abruptly acute; leaves mostly less than 12 cm. long ..... 86. P. TUBERCULATUM
ee. Leaf apex gradually acute to acuminate; leaves commonly 15 cm. or more long (shorter in var.) ..... 87. P. ARBOREUM
bb. Leaf base mostly essentially equilateral or sometimes oblique or with one side slightly shorter.
c. Leaves mostly 7–9 cm. long; spikes scant 2 cm. long ..... 88. P. SUBREPENS
cc. Leaves mostly 10–15 cm. or more long; spikes longer (short in *P. candelarianum*).
d. Petiole strongly vaginate-winged to the blade; leaves bronzed beneath, nerves prominently submarginally loop-connected; peduncle scarcely 5 mm. long ..... 89. P. CORDULATUM
dd. Petiole usually not vaginate-winged to the blade though sometimes grooved above; leaves green or brown but not bronzed.
e. Bracts cupulate, glabrous; fruit free on the rachis, exserted, very short stylose ..... 3. P. DARIENENSE
ee. Bracts more or less peltate; fruit congested on the rachis.

f. Leaves mostly less than 5 cm. wide.
g. Leaves obviously glandular-dotted beneath.
h. Spikes 5 cm. or more long; stigmas sessile..... 90. P. ACUTISSIMUM
hh. Spikes less than 3 cm. long; fruit short-stylose..... 12. P. CANDELARIANUM
gg. Leaves not obviously glandular-dotted.
h. Stems glabrous..... 91. P. PERLASENSE
hh. Stems densely hairy..... 92. P. VIA-CHICOENSE
ff. Leaves 6 cm. or more wide..... 93. P. GRANDE

83. PIPER AUGUSTUM Rudge, Pl. Guian, Rar. 1:10, *pl. 7*. 1805.

Piper angustum Rudge ex Spreng. Syst. Veg. 1:108. 1825, sphalm.
Artanthe augusta Miq. Syst. Pip. 398. 1844.
Artanthe calocoma Miq. in Seem. Bot. Voy. Herald, 199. 1854.
Piper pedicellare C.DC. in Jour. Bot. 4:211. 1866.
Piper calocoma C.DC. in DC. Prodr. 16[1]:264. 1869.

A glabrous shrub, 2–3 m. tall, or small tree up to 8 m., branches somewhat nodose, with moderate internodes; leaves elliptic-ovate, 9–15 or 18 cm. wide × 15–35 cm. long, apex acute, base acute or obtusish, usually subequilateral, pinnately nerved throughout, the nerves 10–16 on each side, not strongly curved upward, densely ciliate, strongly glandular-dotted, drying membranous, translucent; petiole 5–10 mm. long or up to 4 cm. on lower leaves; spikes when young 3 mm. thick × 4–5 cm. long, becoming 1–1.5 cm. × 8–12 cm. when mature; peduncle 1–2 or 3 cm. long; bracts sublunate-triangular-subpeltate, marginally yellow-fringed; fruit oblong, compressed-angular, truncate; stigmas sessile.

Northern South America and Panama.

COCLÉ: Bismarck, above Penonomé, alt. 600–900 m., *Williams 332, 611*. CANAL ZONE: in forest along the Río Indio de Gatún, *Pittier 2790, 2791*.

83a. PIPER AUGUSTUM var. **cocleanum** (Trel.) Yuncker, comb. nov.

Piper polyneurum C.DC. in Candollea 1:270. 1923, name only in index; Schroeder, loc. cit. 3:138. 1926.
Piper gatunense Trel. in Contr. U. S. Nat. Herb. 26:27. 1927.
Piper ladrillense Trel. loc. cit. 1927.
Piper gatunense var. *cocleanum* Trel. in Ann. Mo. Bot. Gard. 27:292. 1940.
Piper gatunense var. *latum* Trel loc. cit. 1940.

Upper internodes sparsely to rather strongly puberulent or pubescent; leaves above from glabrous to rather strongly white-villous, puberulent to villous beneath, at least along the nerves.

Panama.

CHIRIQUÍ: forests along the Río Ladrillo and vicinity, above El Boquete, alt. 1200–1300 m., *Pittier 3164*. COCLÉ: north rim, vicinity of El Valle de Antón, alt. 600–1000 m., *Allen 1784, 1808*. CANAL ZONE: Gatún, *Hayes 502;* hills north of Frijoles, *Standley 27465, 27491, 27495*.

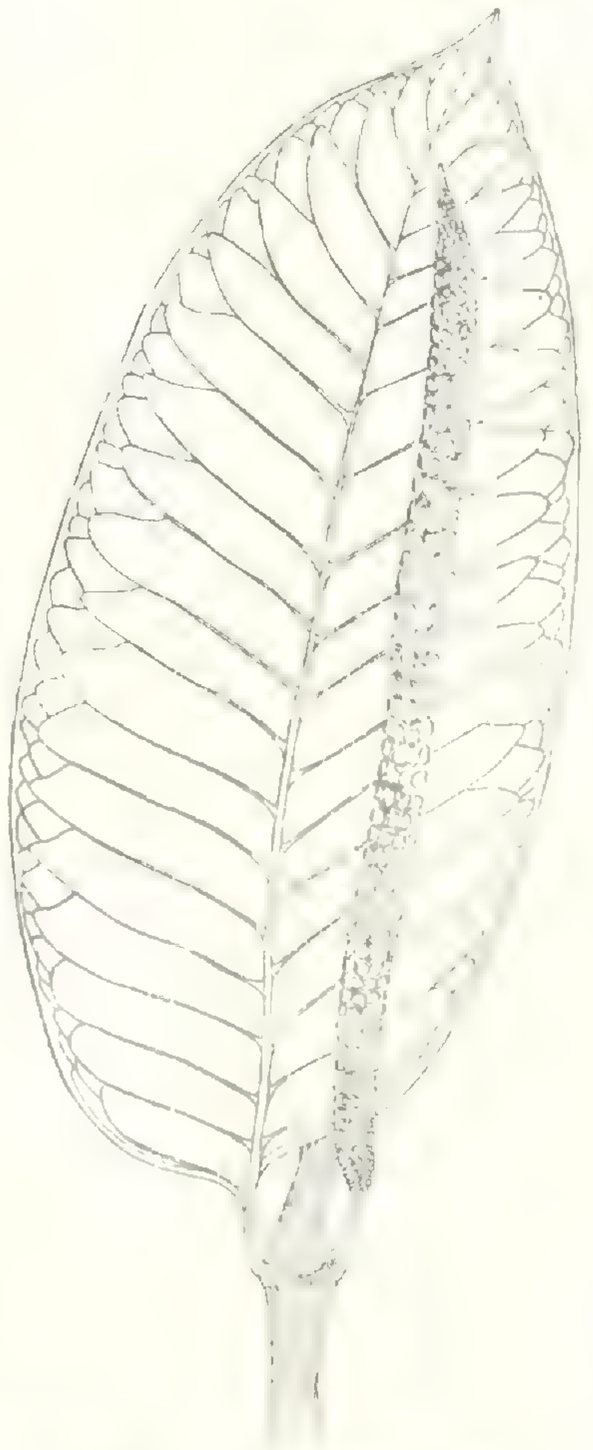

Fig. 12. *Piper augustum* var. *cocleanum*

DARIÉN: Cerro de Garagará, Sambú Basin, alt. 500–974 m., *Pittier 5977* (U. S. Nat. Herb., TYPE).

This species is to be identified because of its large, strongly pinnately nerved, densely ciliate, glandular-dotted leaves, and thick spikes. The original *P. augustum* of Rudge, so far as can be determined, was entirely glabrous. Variety *cocleanum* has pubescent stems and more strongly pubescent leaves. Standley's *Nos. 27465* and *27491* are conspicuously white-villous. No other differences have been noted, however.

84. PIPER STEVENSI Trel. in Contr. U. S. Nat. Herb. 26:27. 1927.

A shrub (?); flowering internodes comparatively long and stout, rather densely subretrorsely crisp-villous; leaves elliptic, apex abruptly short-acuminate, base inequilateral, one side 5–10 mm. shorter and acute, the longer side rounded to the petiole, 10–12 cm. wide × 20–23 cm. long, pinnately nerved to the upper fourth or nearly throughout, with intermediate cross-connecting nervules, the nerves 7–8 on each side, finely scabrous, sparsely to moderately crisp-pubescent on both sides, the nerves densely hirsute, sparingly glandular-dotted beneath, drying papery, translucent, finely pellucid-dotted; petiole 20 plus 5–10 mm. long, vaginate to the middle or above, densely crisp-hairy; spikes 5 mm. thick × 7–8 cm. long; peduncle 1.5–2 cm. long, densely subretrorsely crisp-hairy; bracts triangular-subpeltate, densely ciliate; fruit oblong, glabrous, stigmas sessile.

Known only from Frijoles, Canal Zone.

CANAL ZONE: Frijoles, *Stevens 1247*.

The rather large, somewhat scabrous, pinnately nerved leaves, dense pubescence, and comparatively thick spikes characterize this species.

85. PIPER COLONENSE C.DC. in Smiths. Misc. Coll. 71^6:11. 1920.

Shrub, 2–5 m. tall, nodose; flowering internodes rather short and thick, puberulent; leaves oblong-elliptic, apex rather abruptly acuminate, base rounded, obtuse or cordulate, one side about 5 mm. shorter, 10–11.5 cm. wide ×25–31 cm. long, pinnately nerved from below the upper fourth, the nerves 6 or 7 on each side, with intermediates and cross-connecting and anastomosing nervules, the nerves on both sides puberulent but more conspicuously so above, drying green, paler and pale glandular-dotted beneath, translucent; petiole stout, 10–15 plus 5 mm. long, puberulent, vaginate to near the blade; spikes 3 mm. thick × 10 cm. long; peduncle 15 mm. long, rather stout, puberulent; bracts rounded-triangular-subpeltate, conspicuously yellow-fringed; ovary glabrous; stigmas filiform, sessile.

Central Panama.

COLÓN: around Dos Bocas, Río Fató valley, alt. 40–80 m., *Pittier 4221*.

The large leaves, puberulent on both sides, puberulent twigs, and vaginate petioles distinguish this species.

86. PIPER TUBERCULATUM Jacq. Collect. 2:2, *pl. 211*. 1788.

Piper macrourum H.B.K. Nov. Gen. & Sp. 1:54. 1815.
Piper nutans Opiz in Presl, Reliq. Haenk. 1:156, *pl. 28, f. 2*. 1830.
Steffensia tuberculata Kunth, in Linnaea 13:614. 1839.
Piper scabrum Willd. in hb. p.p., fide Kunth, loc. cit. 1839.
Piper obliquum Balbis in hb., fide Kunth, loc. cit. 1839.
Artanthe decurrens Miq. Syst. Pip. 402. 1844.
Artanthe tuberculata Miq. loc. cit. 497. 1844.
Piper tuberculatum var. *rigido-membranaceum* C.DC. in DC. Prodr. 16^1:266. 1869.

A very nodose shrub or small tree, 2–4 or sometimes up to 6 or 7 m. tall; branches often warty, puberulent when young or less commonly glabrous; leaves subelliptic, subovate, or mostly elliptic-oblong, 3–6 or occasionally up to 10 cm. wide × 7–14 cm. long, apex shortly and rather abruptly acute, base rounded, one side 5–10 mm. shorter at the petiole, the shorter side more elliptic and slightly wider than the longer side, pinnately nerved to near the apex, the nerves 8–10 on each side, with intermediates, rather prominent beneath, glabrous or sparsely puberulent above, puberulent beneath, at least along the nerves, or rarely glabrate, drying membranous, somewhat translucent, obscurely minutely pellucid-dotted; petiole about 5–10 plus 5–10 mm. long, vaginate and narrowly winged throughout with the wings acutely protracted at the base of the blade; spikes 3–5 mm. thick × 5–10 or 12 cm. long; peduncle mostly 10–15 mm. long, rarely up to 2 or 3 cm.; bracts triangular-subpeltate, marginally fringed; fruit somewhat tetragonous, glabrous; stigmas 3, sessile.

West Indies, Central America, and throughout northern South America.

PANAMÁ: without location, *Hayes 802; Bro. Heriberto 267*. CANAL ZONE: Balboa, *Standley 25409;* near Bojii Station, Panama R. R., *Hayes 1017;* Empire, *Stevens 1143; Miller 1863;* near Gorgas Memorial Laboratory, *White 84;* western slope of Ancón Hill, vicinity of Balboa, alt. 20–75 m., *Seibert 119;* Las Cruces Trail, government forest, alt. 75 m., *Hunter & Dodge 759*. PANAMÁ: along the Río Chilibre, *Piper 5681;* vicinity of Bella Vista, *Piper 5375;* along Río Juan Díaz, above Juan Díaz, alt. 30 m., *Allen 943;* Taboga Island, *Miller 2041;* alt. 0–350 m., *Allen 1287;* alt. 0–186 m., *Woodson, Allen & Seibert 1508;* Perlas Archipelago, Saboga Island, *Miller 1950*.

86a. PIPER TUBERCULATUM var. MINUS C.DC. in DC. Prodr. 16^1:266. 1869.

Leaves smaller, mostly 3–7 or sometimes 8 cm. long.

Occurs with the species.

COCLÉ: Penonomé and vicinity, alt. 15–300 m., *Williams 73, 1155*. CANAL ZONE: near Gorgas Memorial Laboratory, *White 84;* Empire, *Miller 1863;* Sabanas north of Panama City, *Bro. Paul 371*.

87. PIPER ARBOREUM Aubl. Hist. Pl. Guian. Fr. 1:23. 1775.

Piper macrophyllum Sw. Prodr. Veg. Ind. Occ. 15. 1788.
Piper geniculatum loc. cit. 1788.
Piper verrucosum loc. cit. 1788.
Piper nitidum loc. cit. 1788.
Piper nodulosum Link in Jahrb. d. Gewächsk. 1^3:62. 1820, name only; Link, Enum. Hort. Berol. 1:36. 1821.
Steffensia xylopioides Kunth, in Linnaea 13:610. 1839.

Piper xylopioides Kunth, loc. cit. 1839.
Steffensia? nitida Kunth, loc. cit. 611. 1839.
Steffensia geniculata Kunth, loc. cit. 612. 1839.
Piper secundum Poepp. in hb. fide Kunth, loc. cit. 1839.
Steffensia? verrucosa Kunth, loc. cit. 613. 1839.
Steffensia Luschnathiana Kunth, loc. cit. 616. 1839.
Piper Luschnathianum Kunth, loc. cit. 617. 1839.
Artanthe Lessertiana Miq. Syst. Pip. 405. 1844.
Artanthe xestophylla Miq. loc. cit. 491. 1844.
Artanthe xylopioides Miq. loc. cit. 492. 1844.
Artanthe geniculata Miq. loc. cit. 493. 1844.
Artanthe Luschnathiana Miq. loc. cit. 494. 1844.
Artanthe verrucosa Griseb. Fl. Br. W. Ind. 171. 1864.
Artanthe macrophylla Griseb. loc. cit. 1864.
Piper arboreum f. *geniculata* Fawc. & Rend., Fl. Jam. 3:23. 1914.
Piper laevibracteum Trel. in Contr. U. S. Nat. Herb. 26:26. 1927.
Piper subnudispicum Trel. loc. cit. 1927.
Piper tuberculatum var. *Alleni* Trel. in Ann. Mo. Bot. Gard. 27:298. 1940.

A glabrous, somewhat nodose shrub, or small tree, mostly 2–7 m. tall; flowering internodes rather short but slender, more or less verrucose-warty; leaves elliptic-ovate, oblong, or lance-elliptic, mostly 6–11 cm. wide × 10–25 cm. long, apex gradually acute to short-acuminate, rounded at base, or narrow leaves acute, one side 5–10 mm. shorter at the petiole, or occasional leaves equilateral, pinnately nerved throughout, the nerves 8–10 on each side with some intermediates; petiole 5–10 plus 5–10 mm. long, vaginate-winged to the blade with the wings protracted beyond the lower blade margin; spikes rather slender and elongated, 2–4 mm. thick and up to 15 cm. long but mostly 5–10 cm.; peduncle 5–10 mm. long and moderately stout; bracts triangular-subpeltate, marginally ciliolate; fruit elongated with the rachis, glabrous; stigmas 3, sessile.

West Indies, northern South America, and Panama.

CHIRIQUÍ: Cerro Vaca, alt. 900–1136 m., *Pittier 5324*. COCLÉ: north rim of El Valle de Antón, alt. 600–1000 m., *Allen 1640*. CANAL ZONE: Barro Colorado Island, Gatún Lake, *Standley 41089*; *Maxon, Harvey & Valentine 6813*; vicinity of Fort Sherman, *Standley 31115*. COLÓN: Loma de la Gloria, near Fató (Nombre de Dios), alt. 10–104 m., *Pittier 4241*.

87a. PIPER ARBOREUM var. **hirtellum** Yuncker, var. nov.

A speciei forma typica differt innovationibus, petiolis, pedunculis, venis subtus plus minusve puberulentis.

Similar to the species except that the young branches, petioles, peduncles, and nerves, especially on the lower surface, are more or less minutely puberulent or hirtellous with erect hairs.—BRITISH GUIANA: NORTHWEST DISTRICT: Waini River, April 3–18, 1923, *de la Cruz 3623* (U. S. Nat. Herb., TYPE).

Northern South America and Panama.

CHIRIQUÍ: vicinity of San Felix, alt. 0–120 m., *Pittier 5131*. CANAL ZONE: hills north of Frijoles, *Standley 27510*. PANAMÁ: Perlas Archipelago, San José Island, *Johnston 424, 594*.

87b. PIPER ARBOREUM var. **falcifolium** (Trel.) Yuncker, comb. nov.

Piper falcifolium Trel. in Contr. U. S. Nat. Herb. 26:25. 1927.

Leaves oblong-lanceolate, 3–5 cm. wide × 10–20 cm. long, apex acuminate, base inequilateral, rounded, obtuse or acute.

West Indies, northern South America, and Panama.

CHIRIQUÍ: Boquete District, alt. 1140 m., *Davidson 618;* vicinity of El Boquete, alt. 1000–1300 m., *Maxon 4959, 5381; Pittier 2958; Bro. Maurice 738;* vicinity of San Felix, alt. 0–120 m., Dec. 1911, *Pittier 5137;* Sabana de la Tortuga, between El Boquete and Caldera, alt. 300–700 m., *Pittier 3327.* PANAMÁ: Perlas Archipelago, San José Island, *Johnston 656, 1373.*

This species appears to be extremely variable in the size of the leaves and to some extent also the shape. Aside from these variations and the presence of short, stiff hairs in one variety, no characters have been discovered by means of which the specific distinctions suggested by the rather long list of synonyms may be maintained. They are believed to be merely varying members of a rather polymorphic species.

88. PIPER SUBREPENS Trel. in Ann. Mo. Bot. Gard. 24:187. 1937.

A nodose, glabrous shrub; flowering internodes short and moderately slender, drying yellowish-glossy; leaves lance-ovate, apex acuminate, base rounded, obtuse, equilateral, or one side very slightly shorter, 2–3.5 cm. wide × 6.5–9 cm. long, pinnately nerved to the upper fourth or nearly throughout, the nerves 3–4 on each side, strongly curving toward the tip submarginally, with intermediates and cross-connecting and anastomosing nervules, the nerves beneath and the midrib above salient, drying firm, glossy, not glandular-dotted, subopaque, narrowly revolute, light green; petiole up to 1 cm. long, glossy, vaginate-winged to the middle or below; spikes 3 mm. thick × 2 cm. long; peduncle slender, up to 1 cm. long; bracts triangular- or rounded-subpeltate, submarginally fringed; fruit obpyramidal-trigonous with dome-shaped apex, glabrous, stigmas filiform, sessile.

Known only from the following locality.

COCLÉ: very near the crest of Cerro Valle Chiquito, alt. 700–800 m., *Seibert 504.*

The short spikes and moderately small leaves with rounded, subequilateral bases distinguish this species.

89. PIPER CORDULATUM C.DC. in Jour. Bot. 4:217. 1866.

Artanthe trinervia Miq. in Seem. Bot. Voy. Herald, 200, *pl. 41.* 1854.
Piper trinerve C.DC. in DC. Prodr. 16[1]:292. 1869, not Vahl, 1804.
?Piper cordulatum var. *granulatum* Trel. in Contr. U. S. Nat. Herb. 26:26. 1927.
Piper san-lorenzanum Trel. loc. cit. 29. 1927.

A glabrous shrub or small tree, 1–3 m. tall; flowering internodes rather slender and short, obscurely finely striate; leaves lanceolate or lance-oblong, apex sharp-acuminate, base rounded or commonly somewhat narrowed downward, one side

usually 1–2 mm. shorter, the longer side cordulate, 3–6 cm. wide × 14–21 cm. long, pinnately nerved throughout, the nerves 7–12 on each side, strongly submarginally loop-connected, the longer nerves prolonged, salient, with cross-connecting and anastomosing nervules, drying rather coriaceous, narrowly revolute, somewhat glossy, usually bronzy-brown beneath, often with fine mottled markings, opaque; petiole 10–20 plus 1–2 mm. long, prominently vaginate-winged to the blade; spikes 3–4 mm. thick × 5–7 cm. long, apiculate; peduncle about 5 mm. long; bracts concave or lunately subpeltate, papillate or glabrous; fruit depressed-obovoid, slightly elongated with the rachis, glabrous, glandular-dotted; stigmas 3, sessile.

Panama.

CANAL ZONE: Gatún Station, *Hayes s. n., 66, 507, 739;* between Gorgona and Gatún, alt. 10–50 m., *Pittier 2207;* Agua Clara Reservoir, *Stevens 589;* around Las Cruces, alt. 20–100 m., *Pittier 2624;* hills north of Frijoles, *Standley 26450, 27578;* Río Paraíso, above East Paraíso, *Standley 29905;* Barro Colorado Island, *Wetmore & Abbe 23; Standley 31355, 40847;* road to Madden Dam and Las Cruces Trail, alt. 75 m., *Hunter & Allen 460.* COLÓN: Chagres, *Fendler 267.* PANAMÁ: thickets and forests near Arraiján, alt. 15 m., *Woodson, Allen & Seibert 782;* Indio, Madden Lake, *Miller 2050, 2065.*

The somewhat bronze-colored leaves with cordulate base, loop-connected nerves, and strongly vaginate-winged petioles distinguish this species.

90. PIPER ACUTISSIMUM Trel. in Contr. U. S. Nat. Herb. 26:25. 1927.

Piper lucaeanum Kunth var. *magnifolium* C.DC. in DC. Prodr. 16[1]:322. 1869.
Piper seducentifolium Trel. in Ann. Mo. Bot. Gard. 27:297. 1940.

A shrub or small tree, 2–3 m. tall, more or less nodose, twigs straight or somewhat zig-zag, glabrous; flowering internodes short and rather slender; leaves lance-elliptic, 2.5–6 cm. wide × 10–18 cm. long, apex acuminate, base subequilaterally acute, pinnately nerved throughout, the nerves 5–8 or 10 on each side, loop-connected upward, glabrous or rather sparsely pubescent along the nerves beneath, drying thin, translucent, glandular-dotted; petiole from 5 mm. long above to 10–15 mm. long below; spikes 3–4 mm. thick × 5–9 cm. long; peduncle filiform, 1–2 cm. long; bracts triangular-subpeltate, sparsely marginally fringed; fruit trigonous, more or less granular-papillate, scarcely longer than thick, truncate-concave at apex; stigmas 3, short, sessile.

Panama and northern South America.

CANAL ZONE: hills north of Frijoles, *Standley 27504, 27590.* COLÓN: Chagres, *Fendler 266.* PANAMÁ: thickets and forests near Arraiján, alt. 15 m., *Woodson, Allen & Seibert 781;* Indio, Madden Lake, *Miller 2060, 2070.* DARIÉN: *Dawe 887.*

90a. PIPER ACUTISSIMUM var. **trichopus** (Trel.) Yuncker, comb. nov.

Piper trichopus Trel. in Contr. U. S. Nat. Herb. 26:25. 1927.

Young growth sparsely to densely pubescent; nerves beneath appressed-pubescent.

Panama.

PANAMA: without location, 1859–60, *Hayes 797* (Herb. New York Bot. Gard., TYPE).

The glabrous twigs, and pinnately nerved, lanceolate, acuminate, and glandular-dotted leaves are distinctive features of this species. It differs from *P. lucaeanum* of Brazil, according to Kunth's description of that species, because of its larger leaves, longer peduncles, and lack of styles. Variety *trichopus* appears to differ only in the pubescence.

91. PIPER **perlasense** Yuncker, sp. nov.

Frutex glaber 2–3 m. altus, caulibus nodosis; internodiis floriferis brevibus gracilibusque; foliis lanceolatis vel sat oblongo-lanceolatis, apice sensim subfalcatim longe acuminatis, basi oblique subinequilateralibus latere altero 1–2 mm. breviore, latere longiore rotundo obtuso, totis vel e quarto supero tantum venosis, venis utrinque 6–8; petiolo deorsum vaginato; spicis 2–3 mm. crassis, 5–6 cm. longis; pedunculo ca. 5 mm. longo; bracteis triangularibus vel rotundato-peltatis margine fimbriatis; drupa parva glabrata obpyramidali-trigona, stigmatibus parvis sessilibus.

A glabrous, nodose shrub 2–3 m. tall; flowering internodes short and slender; leaves lanceolate or somewhat oblong-lanceolate, apex rather gradually subfalcately long-acuminate, base obliquely slightly inequilateral with one side 1–2 mm. shorter and acute, the longer side rounded and obtuse, 2–4.5 cm. wide × 9–15 cm. long, pinnately nerved to the upper one-fourth or throughout, the nerves 6–8 on each side, with intermediates, divergent at the midrib then strongly curved upward and submarginally loop-connected, drying papery, light green, somewhat glossy, translucent; petiole scarcely 5 plus 1–2 mm. or occasionally 1 cm. long, vaginate toward the base; spikes 2–3 mm. thick × 5–6 cm. long when mature; peduncle about 5 mm. long; bracts triangular- or rounded-subpeltate, fringed; fruit small, obpyramidal-trigonous, glabrous, stigmas small, sessile.

Panama.

CANAL ZONE: Barro Colorado Island, *Stevens 7*. PANAMÁ: Perlas Archipelago, San José Island, *Johnston 134, 262, 717;* Jan. 22, 1946, *Johnston 1215* (Herb. Univ. Ill., TYPE), *1327*.

This species appears to be rather closely related to *P. aequale* of South America from which it differs, however, because of its mostly smaller, lanceolate leaves which are more definitely pinnately nerved, and rounded on one side at the base.

92. PIPER **via-chicoense** Yuncker, sp. nov.

Frutex (?); internodiis floriferis gracilibus brevibusque, conferte villosis, pilis usque ad 1 mm. longis plus minusve heteromorphis, brevioribus longioribusque intermixtis; foliis elliptico-vel lanceolato-oblongis, apice acuminatis, basi obtusis vel pro more cordulatis, totis pinnatim venosis, venis utrinque 5 vel ultra, supra glabratis vel ad basem dissite pubescentibus, subtus crispe pubescentibus, venis conferte indutis, pilis dissitis longioribus; petiolo vix 5 mm. longo, conferte hirsuto, basi vaginato; spicis immaturis, 2 mm. crassis, 5 cm. longis, mucronatis; pedunculo 5 mm. longo, pubescente; bracteis triangulari-subpeltatis, margine fimbriatis; ovario ovoideo (?); stigmatibus sessilibus; drupa ignota.

Fig. 13. *Piper via-chicoense*

Shrub (?); flowering internodes short and slender, densely hairy, hairs of various lengths, the longest up to 1 mm. long; leaves elliptic- or lance-oblong, apex acuminate, base with one side slightly shorter at the petiole, both sides obtuse or mostly cordulate, 3–4.5 cm. wide × 10–13 cm. long, pinnately nerved throughout, the nerves 5 or more on each side, more prominent downward, submarginally loop-connected, with cross-connecting-anastomosing nervules, glabrous above or sparsely pubescent at the very base, crisp-pubescent beneath, the nerves densely so and with interspersed long hairs, drying firm, subopaque; petiole scant 5 mm. long, densely hairy, vaginate at the base; spikes as yet young, 2 mm. thick × 5 cm. long, mucronate; peduncle 5 mm. long, pubescent; bracts triangular-subpeltate, marginally fringed; ovary ovoid (?); stigmas sessile; fruit not developed.

Known only from the type locality.

CANAL ZONE and adjacent PANAMÁ: forests along telephone cable trail between splice S16 and S49, Río Indio, Chico Trail, Jan. 12, 1935, *Steyermark & Allen 17431* (Herb. Missouri Bot. Gard., TYPE).

93. PIPER GRANDE Vahl, Eclog. Amer. 2:3, *pl. 11*. 1798.

Piper grandifolium H.B.K. Nov. Gen. & Sp. 1:46. 1815.
Piper riparium H.B.K. loc. cit. 48. 1815.
Schilleria riparia Kunth, in Linnaea 13:707. 1839.
Schilleria grandifolia Kunth, loc. cit. 709. 1839.
?Piper granatense D. Dietr. Syn. Pl. 1:117. 1839.
Artanthe grandifolia Miq. Syst. Pip. 408. 1844.
Artanthe riparia Miq. loc. cit. 409. 1844.
Piper pseudo-variabile Trel. in Contr. U. S. Nat. Herb. 26:23. 1927.
Piper pseudo-variabile var. *pachypus* Trel. loc. cit. 24. 1927.
Piper pseudo-variabile var. *collium* Trel. loc. cit. 1927.
Piper marmoreum Trel. in Ann. Mo. Bot. Gard. 24:186. 1937.
Piper spissinervium Trel. fide Bro. Tomás Alberto in Colegio San José, Medellin, Colombia. Publ. 53–70, p. 18. 1942, name only.

A glabrous shrub or small tree, up to 5 m. tall; flowering internodes slender and moderately elongated; leaves ovate with the midrib commonly somewhat nearer one side, 8–23 cm. wide × 16–30 cm. long, or some leaves may be slightly smaller, apex abruptly acuminate, base nearly equilaterally rounded, the upper acute or subacute, the larger lower leaves obtuse to subcordulate, or occasionally cordate, pinnately nerved to the upper one-third or essentially throughout, the nerves 6–8 or 10 on each side, with shorter intermediates, commonly yellow and prominent

beneath, the lowermost 2 or 3 pairs more or less approximated at the base, drying chartaceous, somewhat glossy, translucent; petiole 10–30 mm. long, the longer vaginate to or beyond the middle; spikes 4–5 mm. thick and up to 15 cm. long; peduncle rather stout, 5–10 mm. long; bracts rounded-subpeltate, umbonate, smooth above, villous beneath; fruit small, obpyramidal-trigonous, apex somewhat dome-shaped; stigmas 3, sessile.

Colombia and Panama.

CHIRIQUÍ: vicinity of San Felix, alt. 0–120 m., *Pittier 5189, 5262.* VERAGUAS: Isla de Coiba, *Mendez 121.* COCLÉ: vicinity of El Valle, alt. 600–1000 m., *Allen 1801;* vicinity of Ola, alt. 100–350 m., *Pittier 5075;* vicinity of El Valle de Antón, alt. 600 m., *Allen 2001.* CANAL ZONE: along Caño Quebrada, *Pittier 6662;* Barro Colorado Island, *Miller 2074; Kenoyer 306; Chrysler 4840; Chardon & Nolla 196; Standley 31308, 40875, 40930, 41054*—a narrow leaved form, *41076;* Río Paraiso, above East Paraíso, *Standley 29892;* Las Cascadas Plantation, near Summit, *Standley 25700, 29518, 29658;* hills west of the canal, near Gatún, *Standley 27191;* hills north of Frijoles, *Standley 27555;* between Frijoles and Monte Lirio, alt. 30 m., *Killip 12145;* Las Cascadas Plantation, near Summit, *Standley 25733;* Battery 46 Hill, Madden Dam road, *Miller 1772, 1773;* vicinity of Fort Sherman, *Standley 31022;* Obispo, *Standley 31702;* Ancón Hill, alt. 180 m., *Williams 19; Standley 25179.* COLÓN: Loma de la Gloria, near Fató (Nombre de Dios), alt. 10–104 m., *Pittier 3845;* along trail to triangulation station on top of Tumba Vieja, alt. 90–200 m., *Dodge, Steyermark & Allen 16924.* PANAMÁ: Pacora River, *Killip 3141;* Río Tapia, *Standley 41188;* Indio, Madden Lake, *Miller 2061, 2062, 2063, 2066;* Río Tapia, *Standley 26130*—the leaves are somewhat smaller and this may represent a large-leaved form of *P. aequale;* Juan Díaz, *Standley 30610, 30577;* Perlas Archipelago, San José Island, *Erlanson 354;* vicinity of Arenosa, lower Río Trinidad, alt. 26–50 m., *Seibert 622.*

The large, ovate, glabrous leaves, drying somewhat glossy, with prominent yellow nerves, and smooth, umbonate floral bracts are distinctive features of this species.

The leaves show considerable variation in size often on the same specimen. The smaller-leaved specimens approach *P. aequale* with which this species is very closely related. These two species may, in fact, represent extremes in leaf size of a single strongly variable species.

VI. KEY TO SPECIES WITH PELTATE LEAVES

a. Petiole 7 cm. or less long, vaginate to the middle or above; mostly with 3 nerves on each side of the midrib above the base.
  b. Leaves strongly bullate-rugose; young growth more or less rusty-tomentose..... 94. P. HARTWEGIANUM
  bb. Leaves not bullate-rugose, not hairy..... 95. P. MAXONII
aa. Petiole 12 cm. long, vaginate at base only; with 2 nerves on each side of the midrib above the base..... 96. P. VERAGUENSE

94. PIPER HARTWEGIANUM (Benth.) C.DC. in DC. Prodr. 16[1]:369. 1869.

Artanthe Hartwegiana Benth. Pl. Hartweg. 254. 1839.
Piper insignifolium C.DC. in Ann. Conserv. & Jard. Bot. Genève 21:242. 1920.
Piper Hayesii Trel. in Contr. U. S. Nat. Herb. 26:39. 1927.

A shrub or small tree, 3–5 m. tall, rusty-villous except for the upper leaf surface which is glabrescent or pubescent along the nerves only; twigs stout; leaves ovate or elliptic-ovate, 16–25 cm. wide × 28–40 cm. long, apex acuminate, base inequilaterally rounded, obliquely retuse or shallowly cordate, peltate 3–6 cm.

from the margin, with 7–9 nerves radiating from the petiole, and the midrib with 3 or 4 branches on each side from the lower half, strongly rugose-bullate, drying firm and subopaque; petiole 5–7 cm. long, vaginate-winged to near the base of the blade; spikes up to 10 mm. thick and 35 cm. long when mature; peduncle 3–4 cm. long; bracts clavate, thickened and bristly at the top, pedicels bearded; fruit oblong-ovate, angular, glabrate; stigmas filiform, sessile.

Southwestern Colombia and Panama.

PANAMÁ: without locality, in 1859–60, *Hayes 705*.

No differences have been found between the above Panamanian specimen and those seen from South America which would justify maintaining *P. Hayesii* as a separate species.

95. PIPER MAXONII C.DC. in Smiths. Misc. Coll. 71[6]:16. 1920.

Piper Whiteae Trel. in Ann. Mo. Bot. Gard. 27:299. 1940.

A glabrous shrub or small tree, 3–6 m. tall; flowering internodes comparatively slender and rather short; leaves 5-sided, rounded-subovate, apex abruptly short-acuminate, base shallowly cordate with one side larger, peltate 1.5–3 cm. above the sinus, 11–18 cm. wide × 16–26 cm. long, pinnately nerved from the lower half with 3 or 4 nerves approximated on each side near the petiole attachment and about 3 branches off each side of the midrib above, the nerves salient beneath with rather prominent cross-connecting and anastomosing nervules, drying rather firm, subtranslucent; petioles mostly 3–6 cm. long, vaginate-winged to near the blade; spikes up to 8 mm. thick × 23 cm. long when mature; peduncles 1.5–2.5 cm. long; bracts rounded-triangular-subpeltate or subcucullate, ciliate; fruit depressed-obovoid, glabrous or sparsely hairy at the top; stigmas linear, subsessile, or on a short, stout style.

Fig. 14. *Piper Maxonii* var. *varium*

Panama.

CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriqui, alt. 1300–2000 m., *Woodson, Allen & Seibert 077*; valley of the upper Rio Chiriqui Viejo, vicinity of Monte Lirio, alt. 1300–1900 m., *Seibert 107*; near El Volcán, *White 177*; vicinity of El Boquete, alt. 1000–1300 m., *Maxon 5050*; along Rio Ladrillo, above El Boquete, alt. 1200–1300 m., *Pittier 3103, 3104*; Chiquero, Boquete District, alt. 1650 m., *Davidson 500*.

95a. PIPER MAXONII var. **varium** (Trel.) Yuncker, comb. nov.

Piper varium Trel. in Ann. Mo. Bot. Gard. 27:299. 1940.

Petioles 4–6 cm. long, vaginate-winged to about the middle; bracts concave with subpeltate apex, glabrous-papillate, or occasionally with one or two short hairs.

Known only from the type locality.

CHIRIQUÍ: trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, alt. 1500–2000 m., *Allen 1491* (Herb. Univ. Ill., TYPE).

96. PIPER VERAGUENSE C.DC. in DC. Prodr. 16^1:294. 1869.

Shrub or small tree (?), glabrous; leaves ovate, apex sharply acuminate, peltate at one-sixth its length above the subcordately rounded base, 14 cm. wide × 28 cm. long, with 10 nerves arising at the petiole and 2 branches ascending off the midrib on either side above; petiole 12 cm. long, vaginate at the base; spikes 3 mm. thick, much shorter than the blade; peduncle 15 mm. long; bracts angularly subpeltate; ovary and fruit not known.

Known only from the one collection.

PANAMA: locality inexact, "Veragua [and Costa Rica?]," *Warscewicz s. n.*

The type of this species has not been examined, and the above description is adapted from the original description and notes made from the type in the Boissier Herbarium by the late Professor Trelease. The peltate leaves with only two pair of lateral nerves above the base, and long petiole vaginate at the base appear to distinguish it sufficiently.

2. OTTONIA Sprengel

OTTONIA Spreng. Neue Entdeck. 1:255. 1820.

Arctottonia Trel. in Proc. Amer. Phil. Soc. 69:315. 1930.

Shrubs; leaves alternate; inflorescence racemose, leaf-opposed as in *Piper;* flowers pedicellate, scarcely crowded; stamens 4–6; ovary more or less 3-angled; stigmas 3; fruit a small, somewhat flask-shaped drupe.

There is some question as to whether the Pipers with racemose rather than spicate inflorescences constitute a genus distinct from *Piper*. So far as known at the present time, the North American species with racemose inflorescences all have palmate nervation and with stamens more or less adhering to the ovary, in contrast to the South American species characterized with pinnately nerved leaves. It is not believed that the differences upon which Trelease based the genus *Arctottonia* are of generic status.

1. OTTONIA **Thiemeana** (Trel.) Yuncker, comb. nov.

Piper Thiemeanum Trel. in Amer. Jour. Bot. 8:214, *pl. 5, f. 2.* 1921.
Arctottonia Pittieri Trel. in Proc. Amer. Phil. Soc. 73:328. 1934.

Fig. 15. *Ottonia Thiemeana*

A loosely branched, glabrous shrub; flowering internodes rather short and slender; leaves ovate, apex gradually long-acuminate, base somewhat obliquely rounded, subobtuse or shallowly cordate, 3–6.5 cm. wide × 8–15 cm. long, palmately 5- to 6-nerved, with slender cross-connecting-anastomosing nervules, drying thin, translucent, slightly rugulose; petiole 3–5 mm. long, vaginate below the middle; racemes about 8 mm. thick × 2–2.5 cm. long; peduncle about 8 mm. long; bracts subspathulate-cupulate, glabrous; pedicels about 2 mm. long; stamens attached at the base of the oblong-ovoid ovary; anthers rather large; ovary somewhat constricted at the apex, glabrous; stigmas commonly 4, short.

Central America.

CANAL ZONE: Alhajuela, May 11–14, 1911, *Pittier 3458* (U. S. Nat. Herb., TYPE).

This specimen appears to agree with the type specimen of the Honduran *Piper Thiemeanum* in all respects.

3. POTHOMORPHE Miquel

POTHOMORPHE Miq. in Bull. Sci. Phys. Nat. Neer. 450. 1840; Comm. Phyt. 36. 1840.

Peperidia Kostel. Allg. Med. Pharm. Fl. 2:455. 1831, not Reichenb. 1828.
Lepianthes Raf. Sylva Tellur. 85. 1838, not *Lepanthes* Sw. 1799.
Heckeria Kunth, in Linnaea 13:564. 1839, not Raf. 1838.

Shrubs or large herbs; leaves large and broad, cordate at the base, or peltate; spikes dense, long and slender, umbellate at the end of an axillary peduncle; flowers sessile, perfect, similar to those of *Piper*. A small genus widely distributed in tropical America.

a. Leaves peltate ..... 1. P. PELTATA
aa. Leaves scarcely peltate ..... 2. P. UMBELLATA

1. POTHOMORPHE PELTATA (L.) Miq. Comm. Phyt. 37. 1840.

Piper peltatum L. Sp. Pl. 30, 1753, sphalm. *pelatum*.
Piper pruinosum H.B.K. Nov. Gen. & Sp. 1:59. 1815.
Piper speciosum H.B.K. loc. cit. 1815.
Peperomia pruinosa Kunth, Pl. Aequin. 1:124. 1822, fide Index Kew.
Peperomia speciosa Kunth, loc. cit. 1822, fide Index Kew.
Piper scutiphyllum Ham. Prodr. Pl. Ind. Occ. 3. 1825.
Peperomia peltata A. Dietr. Sp. Pl. 1:142. 1831.
Peperomia scutata A. Dietr. loc. cit. 143. 1831.
Piper scutatum Willd. in A. Dietr. Sp. Pl. 1:143. 1831, as synonym.
Lepianthes peltatum Raf. Sylva Tellur. 85. 1838.
Heckeria peltata Kunth, in Linnaea 13:565. 1839.

Heckeria scutata Kunth, loc. cit. 567. 1839.
Heckeria speciosa Kunth, loc. cit. 568. 1839.
Pothomorphe scutata Miq. Comm. Phyt. 37. 1840.
Pothomorphe speciosa Miq. loc. cit. 1840.
Pothomorphe Ottonis Miq. Syst. Pip. 207. 1843.
Piper Ottonis C.DC. in DC. Prodr. 16[1]:332. 1869.
Pothomorphe almirantensis Trel. in Ann. Mo. Bot. Gard. 27:306. 1940.
Pothomorphe Baileyorum Trel. loc. cit. 1940.
Pothomorphe Baileyorum var. *paucispica* Trel. loc. cit. 1940.
Pothomorphe tecumensis Trel. loc. cit. 1940.
Pothomorphe tecumensis var. *grandis* Trel. loc. cit. 307. 1940.

Shrub or subshrub, commonly 1–2 m. high; internodes glabrous; leaves rounded-cordate or subdeltoid with retuse base, apex acute, peltate at one-fourth to one-third above the base, mostly with 11–15 nerves radiating from the base of the petiole and usually with one or two pairs arising off the midrib below the middle, the nerves near the margin sparsely to densely short-hairy, and sometimes with a few scattered soft, white hairs above, otherwise glabrous, drying membranous, translucent, yellow-glandular-pellucid-dotted; petiole 9–20 cm. long, vaginate-winged from one-fourth to one-half its length, glabrous; flowering stalks axillary, 4–7 cm. long, glabrous, naked except for the linear-lanceolate bracts at the base of the spikes; spikes umbellate, 2–4 mm. thick × 5–10 cm. long; peduncles slender, commonly about 10–15 mm. long, glabrous; bracts triangular-peltate, marginally fimbriate; flowers sessile, perfect, 2-androus; fruits minute, obpyramidal-trigonous, stigmas 3, minute, sessile.

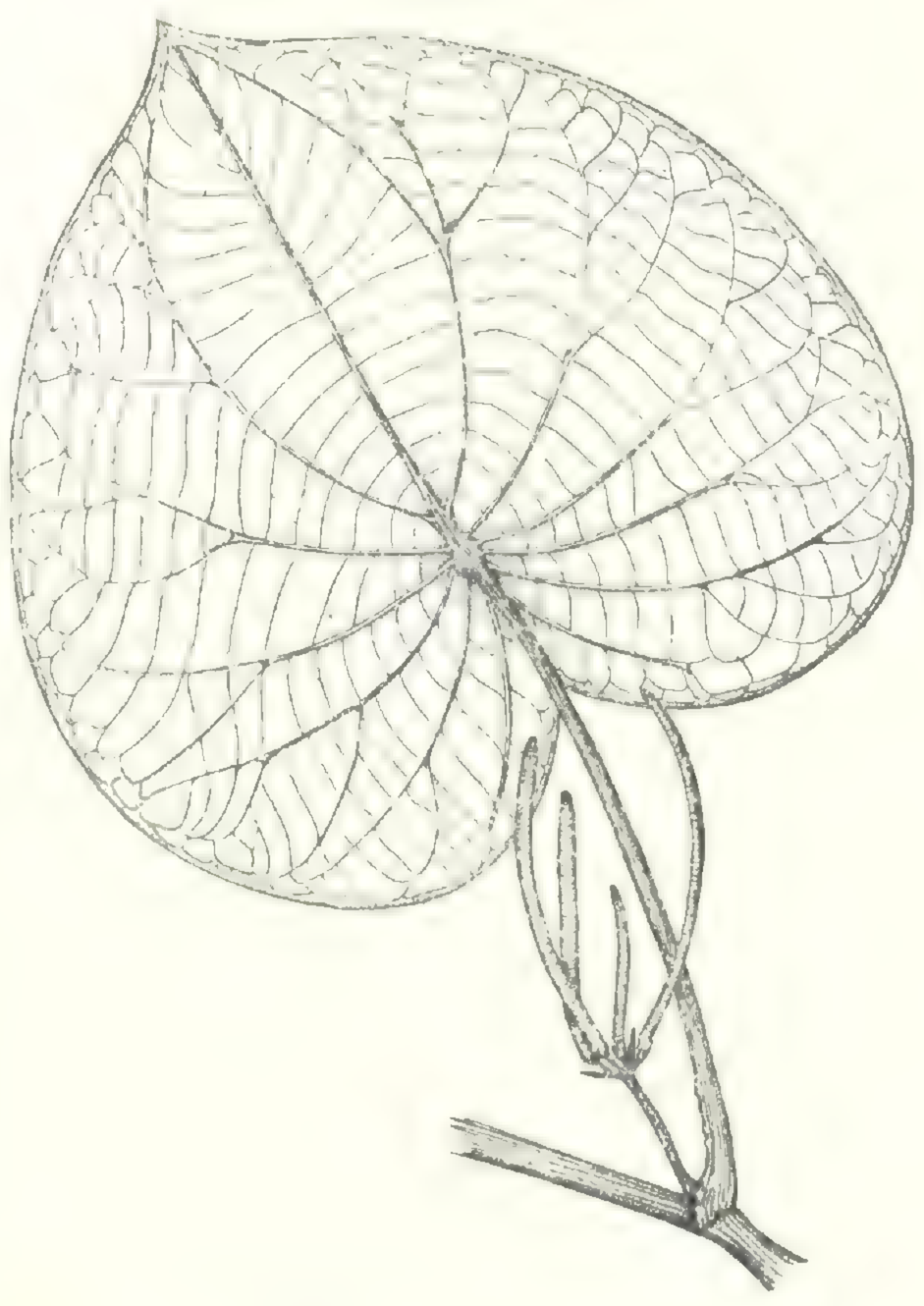

Fig. 16. *Pothomorphe peltata*

Throughout most of the range of the family in the West Indies and the Americas.

BOCAS DEL TORO: Old Bank Island, vicinity of Chiriquí Lagoon, *von Wedel 2025;* Changuinola Valley, *Dunlap 190;* Río Cricamola, between Finca St. Louis and Konkintoë, alt. 10–50 m., *Woodson, Allen & Seibert 1875.* CHIRIQUÍ: Boquete District, Chiquero, alt. 1650 m., *Davidson 512;* Cerro de la Plata, near San Felix, alt. 120–150 m., *Pittier 5160.* COCLÉ: El Valle de Antón, vicinity of Finca Tomás Arias, alt. 600 m., *Allen 3619;* Llano Bonito, north of Las Margaritas, alt. 400–500 m., *Seibert 517.* CANAL ZONE: Chagres, *Fendler 264;* vicinity of Salamanca Hydrographic Station, Río Pequení, alt. 80 m., *Woodson, Allen & Seibert 1573;* vicinity of Madden Dam, near Río Chagres, alt. 50–75 m.,

Seibert 545; Gamboa, *Standley 28525;* Frijoles, *Standley 27619;* between Frijoles and Monte Lirio, alt. 30 m., *Killip 12117;* Monte Lirio, *Maxon 6858;* Las Cascadas Plantation, near Summit, *Standley 25797;* near Old Fort Lorenzo, mouth of Río Chagres, *Piper 5929;* Juan Mina, *Piper 5689;* Barro Colorado Island, Lutz Trail, *Shattuck 2; Kenoyer 305;* Colón to Empire, Panama Railroad, *Crawford 562;* Gatún Station on Panama Railroad, *Hayes 243;* near Río Medio, Battery 46 Hill, *Miller 1774;* vicinity of Fort Sherman, *Standley 30969;* hills west of the Canal, near Gatún, *Standley 27257;* Balboa, *Standley 25602;* Balboa Heights, *Killip 3064.* COLÓN: along Río Sirri, Trinidad Basin, alt. 20–50 m., *Pittier 4016.* PANAMÁ: near Arraiján, alt. 15 m., *Woodson, Allen & Seibert 1398;* Camino de la Granja, *Bro. Heriberto 168;* Río Tecúmen, *Standley 26735;* Río Tapia, *Standley 28062.* DARIÉN: Boca de Cupe, *Williams 697;* vicinity of Yapé, alt. 30 m., *Allen 863;* near the mouth of Río Yapé, alt. 20 m., *Allen 342.*

2. POTHOMORPHE UMBELLATA (L.) Miq. Comm. Phyt. 36. 1840.

Piper umbellatum L. Sp. Pl. 1:30. 1753.
Piper peltatum Ruiz & Pav. Fl. Peruv. & Chil. 1:38, *pl. 59.* 1798, not L. 1753.
Piper sidaefolium Link & Otto, Ic. Pl. Sel. Rar. 15, *pl. 6.* 1820–28, fide Index Kew.
Peperomia umbellata Kunth, Syn. Pl. Aequin. 1:124. 1822, fide Index Kew.
Peperomia sidaefolia A. Dietr. Sp. Pl. 1:141. 1831.
Lepianthes umbellatum Raf. Sylva Tellur. 84. 1838.
Heckeria umbellata Kunth, in Linnaea 13:569. 1839.
Heckeria sidaefolia Kunth, loc. cit. 1839.
Pothomorphe sidaefolia Miq. Comm. Phyt. 36. 1840.
Pothomorphe Dombeyana Miq. Syst. Pip. 211. 1843.
Piper Dombeyanum C.DC. in DC. Prodr. 16[1]:332. 1869.
Piper umbellatum var. *majus* C.DC. loc. cit. 333. 1869.
Pothomorphe Alleni Trel. in Ann. Mo. Bot. Gard. 27:306. 1940.

A soft-wooded shrub, commonly about 2–3 m. high; flowering internodes from densely rusty-villous to soft-puberulent and commonly more or less hairy in lines; leaves round-ovate or reniform, commonly about 20–25 cm. wide × 18–20 cm. long, sometimes much larger, apex subacute to acute, base openly cordate, about 13- to 15-nerved from the base, the midrib with 2 or 3 branches 1–3 cm. above the base, more or less puberulent or pubescent on both sides especially along the nerves, glandular-dotted, drying membranous, translucent, pellucid-dotted; petiole up to 20 cm. long, vaginate-winged to about the middle; flowering branches axillary, puberulent, about 15 mm. long, or occasionally up to 4 cm.; spikes umbellate, rather slender, 3–4 mm. thick and up to 10 cm. long; peduncle scarcely 10 mm. long, puberulent; bracts triangular-peltate, marginally ciliate; stamens 2; fruits minute, obpyramidal-trigonous; stigmas 3, sessile.

West Indies and on the mainland from Mexico to Brazil and Peru.

CHIRIQUÍ: forests around El Boquete, alt. 1000–1300 m., *Pittier 3133.* COCLÉ: vicinity of El Valle, alt. 600–1000 m., *Allen 1190.*

4. SARCORHACHIS Trelease

SARCORHACHIS Trel. in Contr. U. S. Nat. Herb. 26:16. 1927.

Trailing or climbing, rather succulent, glabrous shrubs; leaves alternate; spikes solitary, axillary; stigmas mostly 4, sessile; fruit a small, 1-seeded drupe, partly immersed in and coalescent with the somewhat fleshy rachis at maturity.

1. SARCORHACHIS NARANJOANA (C.DC.) Trel. in Contr. U. S. Nat. Herb. 26:17. 1927.

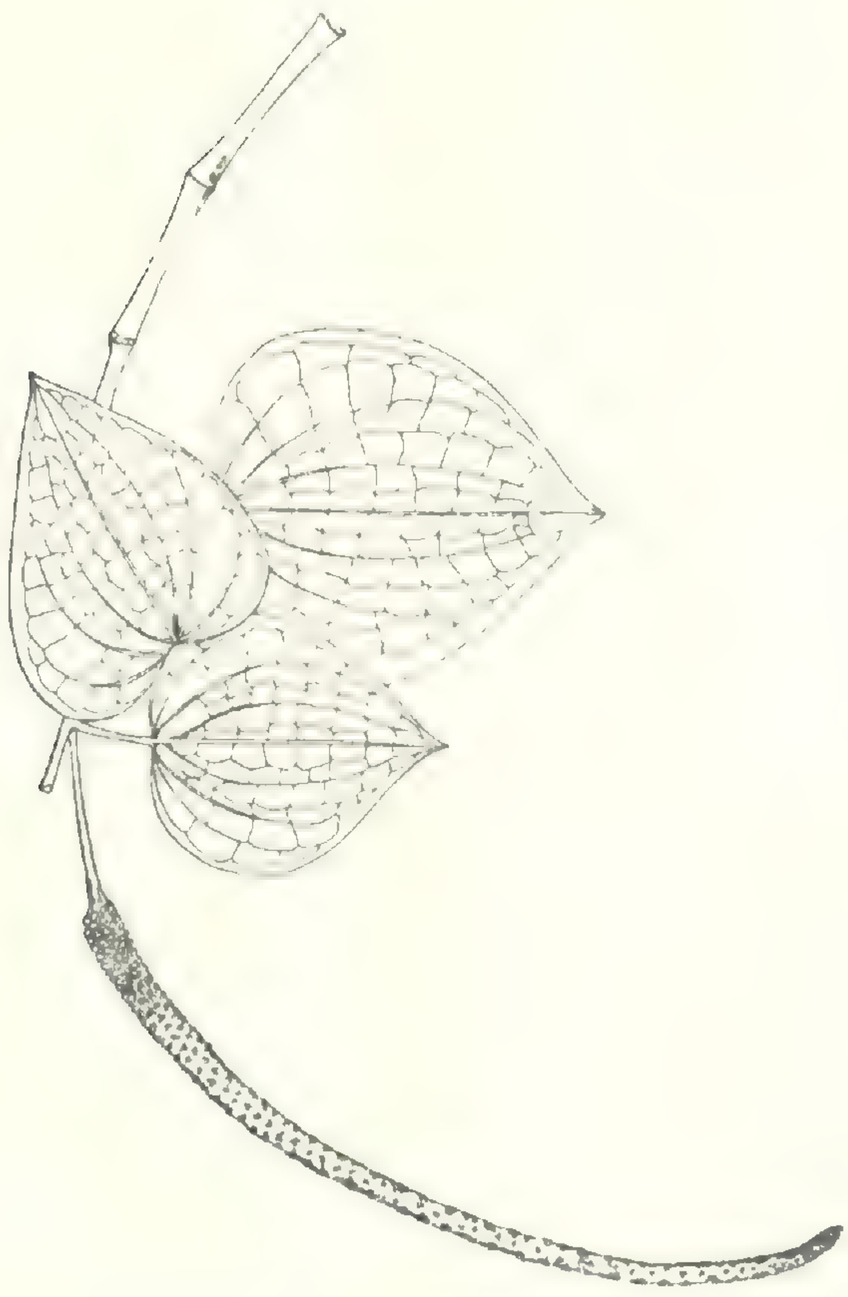

Fig. 17. *Sarcorhachis naranjoana*

Piper naranjoanum C.DC. in Linnaea 37:363. 1872.

Climbing shrub, glabrous; flowering internodes rather short and stout; leaves broadly ovate, apex bluntly short-acuminate, base rounded, truncate, or the lowest subcordate, 6–10 cm. wide × 8–12 cm. long, subpalmately 7- to 9-nerved, the innermost pair of lateral nerves coalescing with the midrib within the lowermost 1 cm.; petiole 1.5–2.5 or sometimes 4 cm. long, vaginate-winged to shortly above the base of the blade; spikes axillary, about 4–8 mm. thick × 13–14 cm. long; peduncle 2–3.5 cm. long, surpassing the adjacent petioles; bracts minute, concave; fruits somewhat flattened laterally, partially imbedded in the rachis, glabrous, stigmas 3–5, comparatively large.

Costa Rica and Panama.

DARIÉN: along the Sambú River, above tide limit, *Pittier 5562*.

This species is quite similar to, if not the same as, *S. incurva* (Sieb.) Trel. of Martinique.

5. ANDERSSONIOPIPER Trelease

ANDERSSONIOPIPER Trel. in Proc. Amer. Phil. Soc. 73:329. 1934.

Soft-wooded shrubs, with flabellately umbellate, axillary spikes, and palmately nerved leaves.

1. ANDERSSONIOPIPER PANAMENSE Trel. in Proc. Amer. Phil. Soc. 73:329, *pl. b.* 1934.

Apparently a moderate-sized half-shrub, glabrous; internodes 8 × 100 mm. long below, shorter and slenderer upward; leaves subreniform, typically abruptly short-acuminate, palmately 13- or 15-nerved with all of the nerves somewhat fine-branched, 10–15 cm. wide × 9–12 cm. long, drying thin, paler beneath; petiole 3–6 cm. long, winged; spikes 2 (or more?), superposed in the axil, curved, in fruit 10 × 100 mm.; peduncle scant 2 × 10 mm.; bracts vague; achenes

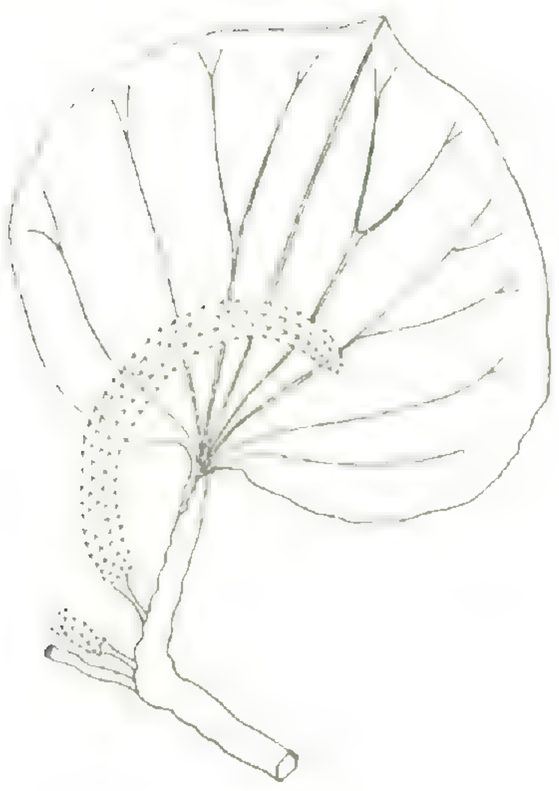

Fig. 18.
Anderssoniopiper panamense

[drupes?] obpyramidal, the contracted apex protruding; stigmas 3, broad, sessile.

Panama.

Known only from the type specimen collected by N. J. Andersson, Apr. 1852, now in the Botanical Museum of Stockholm.

No other specimen of this interesting species has been seen, and there is some question regarding its occurrence in Panama. The above description is copied from that of Prof. Trelease who further states: ". . . there are reported contradictions in the labeling of Andersson's collections, so that while its characters are firmly established, the exact geographic source of the genus now named for him requires confirmation."

6. PEPEROMIA Ruiz & Pavon

PEPEROMIA Ruiz & Pav., Prodr. Fl. Peruv. 8. 1794.

Prostrate, assurgent or erect, succulent, terrestrial or epiphytic herbs; leaves alternate, opposite, or whorled, simple, entire, sometimes peltate, glabrous or more or less hairy, commonly yellow- or black-glandular-dotted, sessile or petiolate, venation palmate, pinnate, or plinerved with the nerves coalescing toward the base; spikes terminal, axillary, or leaf-opposed, slender, sometimes up to 15 cm. or more long; flowers sessile, in the axils of more or less round, peltate bracts, perfect, perianth none, stamens 2, ovary 1, with obliquely scutelliform, rounded-mammiform, somewhat stylose, or rostrate beak; stigma apical or subapical; fruit very small, globose, ellipsoidal, or subcylindrical, one-seeded, drupe-like, with a thin pericarp and somewhat hardened endocarp, commonly verrucose and viscid.

PRIMARY KEY TO SPECIES OF *PEPEROMIA*

a. Spikes solitary, or few (2–4) on a common stalk, scarcely paniculate.
  b. Leaves scarcely peltate (the margin may join across the petiole in some species).
    c. Fruit essentially sessile.
      d. Fruit and ovary apically more or less mammiform or stylose; stigmas essentially apical.
        e. Leaves alternate, mostly membranous; fruit lacking a pseudocupule ..... I. Spp. 1–10 (pp. 77–82)
        ee. Leaves mostly 3–4 at a node (sometimes 2); fruit with a pseudocupule ..... II. Spp. 11–19 (pp. 82–87)
      dd. Fruit and ovary apically oblique; stigma subapical, anterior.
        e. Fruit globose-ovoid, short-pointed, subbasally attached ..... III. Spp. 20–47 (pp. 88–102)
        ee. Fruit ellipsoidal or cylindrical, attached basally, apex obliquely scutelliform or rostrate ..... IV. Spp. 48–57 (pp. 103–111)
    cc. Fruit stipitate ..... V. Sp. 58 (p. 111)
  bb. Leaves distinctly peltate ..... VI. Spp. 59–66 (pp. 112–116)
aa. Spikes numerous, paniculate ..... VII. Spp. 67–72 (pp. 117–120)

I. KEY TO SPECIES WITH FRUIT ATTACHED BASALLY, LACKING PSEUDOCUPULE, APICALLY MORE OR LESS MAMMIFORM OR STYLOSE, AND WITH STIGMAS APICAL OR SLIGHTLY SUBAPICAL.

(Subgenus TILDENIA Miq. in part).

a. Leaves pinnately nerved or pli-nerved.
  b. Margin of floral bracts entire or only slightly irregular.
    c. Leaves mostly 15 cm. or more long..... 1. P. ADSCENDENS
    cc. Leaves mostly 10–12 cm. or less long..... 2. P. ACUMINATA
  bb. Margin of floral bracts ciliate..... 3. P. CILIOLIBRACTEA
aa. Leaves palmately nerved or slightly plinerved near the base only.
  b. Leaves and stems glabrous.
    c. Leaf apex obtuse; stems short; fruit not longitudinally ribbed.
      d. Leaves 5- to 7-nerved; base cordulate..... 4. P. BREVIPEDUNCULA
      dd. Leaves 9- to 11-nerved; base cordate..... 5. P. PSEUDO-DEPENDENS
    cc. Leaf apex acute; stems erect, branching.
      d. Midrib obviously branched upward; leaves mostly 1.5–2.5 cm. wide..... 6. P. PELLUCIDA
      dd. Midrib scarcely branched upward; leaves mostly 3 cm. or more wide..... 7. P. CORDULATIFORMIS
  bb. Leaves and petioles hairy.
    c. Leaves 3–5 cm. or more long.
      d. Leaves less than 4 cm. wide; spikes much longer than the leaves.... 8. P. INSUETA
      dd. Leaves much wider; spikes shorter than the leaves..... 9. P. UMBRIGAUDIENS
    cc. Leaves mostly scarcely 1.5 cm. long, mostly hirtellous..... 10. P. PANAMENSIS

1. PEPEROMIA ADSCENDENS C.DC. in Jour. Bot. 4:140. 1866.

Peperomia glabra C.DC. loc. cit. 143. 1866.
Peperomia casitana Trel. in Ann. Mo. Bot. Gard. 27:301. 1940.
Peperomia sarcodes Trel. loc. cit. 304. 1940.

A rather large, assurgent, epiphytic or occasionally terrestrial, glabrous herb; stem few-leaved, 5–10 mm. thick when dry, ascending to 10–15 cm. or more, internodes mostly scarcely 10 mm. long, leaf scars large; leaves alternate, broadly oblanceolate, 5–9 cm. wide × 15–25 or even 30 cm. long, apex acuminate, often abruptly so, base cuneate-decurrent, pinnately nerved, midrib prominent, lateral nerves inconspicuous; petiole 1–4 cm. long, margined by the decurrent blade; spikes terminal, 5 or 6 mm. thick and up to 25 cm. or more long, densely flowered; peduncle 15–20 mm. long, commonly with a small leaf or bract near the middle; floral bracts round-peltate; fruit about 1 mm. long, ellipsoidal, yellow at the base, abruptly and truncately short-pointed; stigma apical.

Northern South America and Central America.

CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., *Woodson, Allen & Seibert 952;* trail from Cerro Punta to headwaters of Río Caldera, alt. 2250–2500 m., *Allen 1452;* Boquete District, Bajo Chorro, alt. 2250 m., *Davidson 206.*

The large, thick, pinnately nerved leaves, long, thick spikes, and fruit shape distinguish this species.

2. PEPEROMIA ACUMINATA Ruiz & Pav. Fl. Peruv. & Chil. 1:32, *pl. 51, f. a.* 1798, not *P. acuminata* (L.) Dahlst. 1900.

Piper acuminatum Pers. Syn. 1:35. 1805, not *P. acuminatum* L. 1753.
Piper nemorosum Vahl, Enum. Pl. 1:341. 1805.
Peperomia pyrifolia H.B.K. Nov. Gen. & Sp. 1:61. 1815.
Peperomia basellaefolia H.B.K. loc. cit. 66. 1815.

Piper basellaefolium Poir. in Lam. Encycl. Meth. 4:Suppl. 468. 1816.
Piper murinum Roem. & Schult. Syst. Veg. 1:325. 1817.
Piper pyrifolium D. Dietr. Encycl. 122. 1831, not *P. pyrifolium* Vahl. 1805.
Peperomia nemorosa C.DC. in DC. Prodr. 16^1:415. 1869.
?*Peperomia dichroophylla* Sodiro, Contr. Conoc. Fl. Ecuator. Monogr. 1. ed. 2. 157. [1901].
Peperomia Ruiziana C.DC. in Candollea 1:301. 1923.
Peperomia Ekmani Trel. in Fedde. Rep. Sp. Nov. 23:31. 1926.
Peperomia acuminatifolia Trel. in Contr. U. S. Nat. Herb. 26:48. 1927.
Peperomia oblanceaelimba Trel. in Badillo in Cat. Fl. Venez. 1:245. 1945, name only.

An assurgent, simple or sparingly branched, glabrous, succulent herb; stem 4–5 or sometimes 10 mm. thick when dry, ascending from the decumbent, rooting base to 60 cm. or more in large specimens; internodes 1–3 or 4 cm. long, leaf scars large, nodes commonly more or less tumid; leaves alternate, elliptic, lanceolate or oblanceolate, 2–4 cm. wide × 6–13 cm. long, apex attenuate and sharply more or less arcuately acuminate, base cuneate, decurrent, pinnately nerved, drying coriaceous and subopaque, commonly minutely dark-dotted and glandular beneath, minutely ciliolate at the apex; petiole 5–10 mm. long, or occasionally 15–20 mm. on lower leaves, more or less winged by the decurrent blade; spikes solitary, terminal, closely flowered, 3–4 mm. thick × 10–13 cm. long; peduncle 3–5 cm. long, sometimes with a small leaf or bract; floral bracts round-peltate; fruit about 1 mm. long, ellipsoidal, abruptly and truncately scutellate, sometimes yellowish at the base, stigma apical.

West Indies, Panama, and northern South America.

PANAMA: without locality, *Hayes 817*.

3. PEPEROMIA CILIOLIBRACTEA C.DC. in Candollea 1:360, 383. 1923.

A moderate-sized, assurgent herb; stem 3–4 mm. thick, ascending to 15 cm. or more from the decumbent, rooting base, velvety pubescent; internodes scarcely 1 cm. long, nodes somewhat tumid, leaf-scars large; leaves alternate, oblong-ovate or subobovate, apex shortly sharp-acuminate, base rounded, cordulate to acute, mostly 2–5 cm. wide × 5–8 cm. long, occasionally up to 7 × 14 cm., puberulent on both sides, rather densely so along the nerves beneath, ciliolate, 9- to 11-plinerved, the uppermost lateral nerves branching off the midrib near the middle, drying membranous, translucent, reddish-glandular-dotted beneath; petiole 2–5 or sometimes up to 8 cm. long, velvety; spikes 2 mm. thick × 10–14 cm. long, closely flowered; peduncle up to 5 cm. long, velvety; bracts round-peltate, reddish-glandular-dotted, marginally more or less ciliate; fruit about 1 mm. long, subglobose, apex pointed, slightly oblique, stigma essentially apical, basal part of the fruit yellowish, upper half reddish with reddish-glandular dots.

Panama.

CANAL ZONE: Las Cascadas Plantation, near Summit, *Standley 25731*; Barro Colorado, *Stevens 637*; Wheeler Trail, *Shattuck 214*. PANAMÁ: Chararé River near Chepo, alt. 50–200 m., *Pittier 4712*.

The plinerved leaves, velvety stems, leaves, etc., short internodes, and shape of fruit are distinctive of this species.

4. PEPEROMIA BREVIPEDUNCULA Trel. in Contr. U. S. Nat. Herb. 26:43. 1927, not *P. Heydei* var. *brevipeduncula* C.DC.

A short, rhizomatous, leafy, glabrous herb; stem ascending 6–8 cm. from a fibrous-rooted, somewhat contorted-nodulose (when dry) rhizome about 4 mm. thick, internodes up to 10 mm. long; leaves alternate, round, round-ovate, or elliptic-ovate, apex rounded or slightly pointed, base cordulate or shallowly cordate, 4.5–6 cm. wide and occasionally up to 9.5 cm. long, palmately 5-nerved, or large leaves 7-nerved with the outermost laterals slender and indistinct, nerves sparingly branched upward, drying dull, membranous, translucent, pellucid-dotted; petiole 2–6 cm. long, clasping; spikes opposite the upper leaves, and axillary, rather stout, 2–3 mm. thick × 8–15 cm. long, rather loosely flowered; peduncle 5–15 mm. long; bracts round-peltate, glandular-dotted; fruit globose, about 1 mm. long, apex mammiform, stigma apical.

Southern Panama.

DARIÉN: Boca de Panarandó, on Sambú River, alt. 20 m., *Pittier 5590*.

When Trelease described this species he considered it as being the same as *P. Heydei* var. *brevipeduncula,* which is now believed to be *P. pseudo-dependens.* It differs from that species because of its fewer-nerved leaves with cordulate rather than cordate base. From *P. Heydei* it differs in the shape of the fewer-nerved leaves, shorter peduncles, etc.

5. PEPEROMIA PSEUDO-DEPENDENS C.DC. in Jour. Bot. 4:137. 1866.

Peperomia Heydei C.DC. var. *brevipeduncula* C.DC. in Ann. Conserv. & Jard. Bot. Genève 21:247. 1920.
Peperomia brevipeduncula (C.DC.) Trel. var. *major* Trel. in Ann. Mo. Bot. Gard. 27:301. 1940.

A short-stemmed, glabrous, succulent, few-leaved herb, perennial from a small corm; leaves alternate, round-ovate, up to 11 cm. in diameter, apex obtuse or subacute, base deeply cordate, palmately 9- to 11-nerved, the nerves forked upward, drying very thin and translucent; petiole up to 10 cm. long, mostly about 5–7 cm.; spikes terminal and axillary, rather loosely flowered, 2–3 mm. thick and up to 14 cm. long; peduncle 7–10 or even 20 mm. long; bracts round-peltate, red-glandular-dotted; fruit about 1 mm. long, globose-ovoid, sulcate ventrally toward the base, apex mammiform, stigma apical.

Venezuela, northern Colombia, and Panama.

PANAMÁ: Río Las Lajas, alt. 20 m., *Allen 2037*.

6. PEPEROMIA PELLUCIDA (L.) H.B.K. Nov. Gen. & Sp. 1:64. 1815.

Piper pellucidum L. Sp. Pl. 30. 1753.
Piper concinnum Haw. Rev. Pl. Succ. 198. 1821.
Peperomia concinna A. Dietr. Sp. Pl. 1:164. 1831.
Micropiper pellucidum Miq. Comm. Phyt. 54. 1840.
Peperomia pellucida var. *pygmaea* Willd. Herb. ex Miq. Syst. Pip. 81. 1843.
Peperomia pellucida var. *minor* Miq. in Mart. Fl. Bras. 4^1:10. 1852.

A rather delicate, erect, glabrous, pellucid, branched herb; stem up to 5 mm. thick near the base and 50 cm. tall; leaves alternate, round-deltoid-ovate, mostly 15–25 mm. wide, apex somewhat attenuate, acute, base subtruncate-cordate, palmately 5-nerved, drying very thin, semi-transparent; petiole mostly 1–2 cm. long, clasping-decurrent; spikes terminal, axillary, or leaf-opposed, slender, 2–5 cm. long, very loosely flowered; peduncle about 5 mm. long; bracts round-peltate; fruit about 0.8 mm. long, ellipsoidal, longitudinally more or less sulcately striate; apex pointed, stigma apical.

A common weedy species occurring throughout the West Indies and tropical North and South America. It is also found in the Old World tropics and Pacific Islands.

Panama: without locality, *Bro. Heriberto 78*. Bocas del Toro: vicinity of Nievecita, alt. 0–50 m., *Woodson, Allen & Seibert 1866*; vicinity of Chiriquí Lagoon, *von Wedel 1256*; lower Changuinola River, *Stork 1*. Canal Zone: Balboa, *Standley 25827, 27150*; *Foster s. n.*; Gatún, *Cowell 202*; Summit, *Stevens 325*; *Standley 26005*; Ancón, alt. 2080 m., *Pittier 3062*; Ancón Hill, *Stevens 704*. Colón: Chagres, *Fendler 302*; vicinity of Porto Bello, alt. 5–10 m., *Pittier 2469*. Panamá: Chepo, alt. 60 m., *Pittier 4450*; Las Sabanas, *Standley 25050*; Taboga Island, *Standley 27063, 27881*; Perlas Archipelago, San José Island, *Johnston 126, 178*. San Blas: vicinity of Puerto Obaldía, alt. 0–50 m., *Pittier 4370*.

This species, together with the East Indian *P. exigua*, constituted the subgenus Ogmocarpidium of Dahlstedt.

7. Peperomia cordulatiformis Trel. in Bot. Gaz. 73:143. 1922.

An ascending, glabrous, rather large herb; stem 3–4 mm. thick when dry, ascending to 50 cm. or more, freely and widely branching, internodes up to 10 cm. long, rooting from the lower nodes; leaves alternate, round-ovate, apex bluntly short-acute, not at all bristly, base rounded, cordate, scarcely peltate as originally described, 3–5 cm. wide × 4–6 cm. long, smaller upward in young growth, palmately 5- to 7-nerved, the midrib scarcely branched upward, drying membranous, translucent, glandular-dotted; petiole up to 5 cm. long on larger, lower leaves, reduced upward with smaller uppermost leaf petioles 5 mm. long, channelled above, clasping-decurrent; spikes leaf-opposed, 1 mm. thick × 4–5 cm. long, rather loosely flowered; peduncle 5–10 mm. long; bracts round-peltate, glandular-dotted; fruit globose-ovoid, about 0.5 mm. long, apex scarcely oblique, stigma essentially apical.

Canal Zone.

Canal Zone: Mamei Hill, alt. 20–90 m., on rocks, *Pittier 3806*; vicinity of Madden Dam, near Río Chagres, alt. 50–75 m., on banks of brook and in water, *Seibert 553*; Alajuela, rocks along Chagres River, *Pittier 3467*.

Trelease described the leaves as "obscurely subpeltate." The margin, however, does not meet over the petiole in the type specimen. It differs from *P. cordata* because of its smaller, non-peltate leaves, and character of fruit. It rather closely resembles *P. pellucida* in many respects but differs because of its usually larger leaves in which the midrib is scarcely branched upward.

8. PEPEROMIA INSUETA Trel. in Ann. Mo. Bot. Gard. 27:303. 1940.

A rather small, terrestrial, acaulescent herb; leaves arising from a short, thickened, rhizome-like base, elliptic, apex obtuse, base obtuse, cordulate, or subacute, 2–4 cm. wide × 4–7.5 cm. long, moderately to sparsely crisp-pubescent above, moderately crisp-pubescent beneath, more densely so along the nerves, scarcely ciliate, palmately 5-nerved, or large leaves with an additional pair of slender nerves at the base, the innermost pair of nerves appearing to coalesce with the midrib within the lowermost 5 mm., the midrib and lateral nerves branched upward, drying darker above, paler beneath, membranous, translucent, glandular-dotted beneath; petiole 3–8 cm. long, crisp-pubescent; spikes 1.5 mm. thick × 6–12 cm. long, rather closely flowered; peduncle about equilong, crisp-pubescent; rachis pubescent at the base and with a few, scattered hairs above; bracts round-peltate, glandular-dotted; fruit about 0.6 mm. long, globose, stigma apical or at most only slightly subapical.

Panama.

COCLÉ: vicinity of El Valle, alt. 600–1000 m., *Allen 1220.* CANAL ZONE: Quebrada Ancha, alt. 70 m., *Dodge & Steyermark 17061; Steyermark & Allen 17061a.*

The acaulescent plants, long-petiolate, elliptic leaves with pubescent blades and petioles, long spikes on long peduncles, and somewhat pubescent rachises are distinctive characters of this species.

9. PEPEROMIA **umbrigaudens** Yuncker, sp. nov.

Herba succulenta rhizomatosa; foliis alternis, rotundato-ovatis usque ad 11 cm. latis, apice obtusis vel subacutis, basi profunde cordatis, sinu aperto, palmatim 11-nerviis supra sat dissite villosis subtus ad venas plus conferte villosis; petiolo usque ad 15 cm. longo, sat gracili, proximo laminae villoso, deorsum glabrato; spicis solitariis; pedunculo ca. 6 cm. longo, dissite villoso; ovario subturbinato, apice submammiformi, stigmate apicali interdum bifido.

A rhizomatous, succulent, shade-loving herb; leaves alternate, few, clustered at the end of a fleshy, fibrous-rooted rhizome 5–10 mm. thick when dry, round-ovate, apex obtuse or obscurely acutish, base deeply cordate with open sinus, up to 11 cm. in diameter, palmately 11-nerved, the nerves strongly forked upward, rather sparsely villous above, more densely so along the nerves beneath, drying thin, translucent, finely pellucid-dotted, paler and prominently glandular-dotted beneath; petiole up to 15 cm. long, rather slender, villous near the blade, glabrescent downward; spikes solitary, terminal (?) or axillary (?), 2 mm. thick × 6 cm. long, closely flowered; peduncle equilong, thinly villous; bracts round-peltate; ovary subturbinate, apex submammiform, stigma apical, sometimes bifid.

Known only from the type locality.

PANAMA: Cerro Trinidad, on moist boulders in deep shade, alt. 800–1000 m., Oct. 20, 1946, *Allen 3766* (Herb. Missouri Bot. Gard., TYPE).

This species resembles *P. pseudo-dependens* in some respects but differs because of the pubescence of the leaves, petioles, and peduncles, longer peduncles, etc.

10. Peperomia panamensis C.DC. in Candollea 1:329. 1923.

A small, spreading, stoloniferous epiphyte; stem branched, 1 mm. thick, fruiting branches ascending to 5 cm., internodes mostly 1–3 cm. long, minutely hirtellous; leaves alternate, suborbicular, round-obovate, or occasionally elliptic-subovate, 6–14 mm. wide × 8–20 mm. long, apex rounded, acute at the very base, palmately 3- to 5-nerved, both sides glabrous or sparsely minutely hirtellous, ciliolate toward the apex; petiole 3–8 mm. long, mostly about 5 mm., sulcate above, clasping, glabrous or minutely hirtellous; spikes terminal and axillary, 2 mm. thick × 10–15 mm. long, closely flowered; peduncles mostly 5–8 mm. long, sparsely minutely hirtellous or glabrate; bracts round-peltate; fruit about 1 mm. long, basally immersed or eventually on pseudopedicels, subturbinate-cylindrical, apically mammiform, stigma apical.

Panama and northern South America.

Coclé: mountains beyond La Pintada, alt. 400–600 m., *Hunter & Allen 574*. Canal Zone: in forest along the Río Indio de Gatún, near sea-level, *Pittier 2789*.

The minutely hirtellous, repent stems, rounded leaves, short spikes, and shape of fruit characterize this species.

II. KEY TO SPECIES MOSTLY WITH OPPOSITE OR VERTICILLATE LEAVES; FRUIT STYLOSE AND WITH A PSEUDOCUPULE.

(Subgenus Micropiper (Miq.) Dahlst.).

a. Leaves scarcely 10–12 mm. long, apex scarcely protracted.
  b. Rachis puberulent ..... 11. P. reflexa var. americana
  bb. Rachis not puberulent.
    c. Stems and leaves glabrous; leaves longer than wide, commonly whorled ..... 12. P. quadrifolia
    cc. Stems and leaves more or less hairy.
      d. Leaves in whorls of 4, round or obovate-elliptic ..... 13. P. quaternata
      dd. Leaves mostly opposite, orbicular ..... 14. P. cyclophylla
aa. Leaves mostly 10–20 mm. or more long.
  b. Leaves about 10–20 mm. long, opposite, apex scarcely narrowed ..... 15. P. quadrangularis
  bb. Leaves mostly much longer, or whorled and constricted toward the apex.
    c. Stem hirtellous; leaves bluntly constricted-pointed; peduncle 4–5 cm. long ..... 16. P. bocasensis
    cc. Stem essentially glabrous, or, if hirtellous, leaves larger, narrowly pointed.
      d. Leaf apex minutely hirtellous; leaves drying rather thin, 3 central nerves prominent ..... 17. P. martagonifolia
      dd. Leaf apex glabrous.
        e. Spikes densely flowered, commonly 6–8 cm. long; bracts contiguous or overlapping; leaves drying coriaceous opaque; spikes often multiple ..... 18. P. Seemanniana
        ee. Spikes loosely flowered, commonly 10 cm. or more long; bracts mostly remote; leaves drying membranous, translucent, spikes mostly solitary ..... 19. P. viridispica

11. Peperomia reflexa (L. f.) A. Dietr. var. americana (Miq.) Dahlst. in Kgl. Sv. Vet.-Akad. Handl. 33^2:175. 1900.

Peperomia reflexa f. *americana* Miq. Syst. Pip. 173. 1843.
Peperomia reflexa var. *enervulosa* C.DC. in DC. Prodr. 16^1:452. 1869, in part (?).
Peperomia americana Herter in Rev. Sudamer. Bot. 6:150. 1940.

A somewhat caespitose or repent, branched, spreading, succulent, epiphytic herb; stems 1–2 mm. thick, fruiting branches ascending up to about 5 cm., internodes variable, commonly 1–4 cm. long, drying angular-grooved, hirtellous-subvillous, the hairs often rather scattered, stiffish, and of varying lengths, up to 1 mm. long; leaves mostly in whorls of 4, rhombic-ovate, ovate, elliptic or suborbicular, commonly 5–10 mm. wide × 8–15 mm. long, apex rounded or slightly contracted, base acutish, glabrous above, loosely subvillous beneath, obscurely palmately 3-nerved, drying coriaceous and subopaque; petiole mostly 1–2 mm. long, subvillous; spikes terminal, densely flowered, 2 mm. thick × 1–3 cm. long; peduncle up to 2–3 cm. long, loosely subvillous; rachis ridges hispid; bracts round-peltate; fruit immersed in pits, about 1 mm. long, subcylindrical, with basal pseudocupule, apex conical, stigma apical.

West Indies and on the mainland from Mexico through Central America and northern South America.

CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., *Woodson, Allen & Seibert 879;* Chiriquí Volcano, Boquete District, alt. 2100 m., *Davidson 875;* El Potrero Camp, alt. 2600 m., *Killip 3603;* Río Caldera, above El Boquete, alt. 1300–1350 m., *Killip 3512;* valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, alt. 1300–1900 m., *Seibert 147;* near Los Siguas Camp, southern slope of Cerro de la Horqueta, alt. 1700 m., *Maxon 5539.*

Plants which are believed to represent the typical form of this species have stems minutely subreflexed-hirtellous with the hairs only 0.1–0.2 mm. long. The contrast in pubescence appears to hold in all of the specimens examined and is the chief character upon which the variety is based.

12. PEPEROMIA QUADRIFOLIA (L.) H.B.K. Nov. Gen. & Sp. 1:69. 1815.

Piper quadrifolium L. Sp. Pl. ed. 2. 1:43. 1762.
Troxirum quadrifolium Raf. Sylva Tellur. 85. 1838.
Peperomia subquadrifolia Trel. in Contr. U. S. Nat. Herb. 26:43. 1927.

A small, glabrous, arboricolous herb; stem 1.5–2 mm. thick, repeatedly forking, rooting from the lower nodes, drying yellowish, somewhat scaly, angular; leaves in whorls of 3–7 but commonly 4 at a node, obovate, oblong-obovate, or obovate-elliptic, emarginate, the notch bristly-hairy, base acute to subcuneate, 5–8 mm. wide × 8–14 mm. long, obscurely palmately 3-nerved, drying coriaceous, opaque, narrowly subrevolute; petiole 1–2 mm. long, channelled above, occasionally microscopically hirtellous; spikes terminal, closely flowered, 1.5 mm. thick × 2–3 cm. long; peduncle 1–2 cm. long, comparatively slender; bracts round-peltate; rachis pitted; fruit obliquely ovoid, about 1 mm. long, acutely narrowed into a short, stout style, with basal pseudocupule, stigma apical.

Mountains of Chiriquí province and elsewhere throughout Central America, the West Indies, and northern South America.

CHIRIQUÍ: Volcán de Chiriquí, vicinity of Casita Alta, alt. about 1500–2000 m., *Woodson, Allen & Seibert 815, 972;* eastern slope, Camp Aguacatal, alt. 2400–2500 m., *Maxon 5298;* vicinity of Cerro Punta, alt. 2000 m., *Allen 1532;* valley of the upper Río Chiriquí

Viejo, vicinity of Monte Lirio, alt. 1300–1900 m., *Seibert 148*; Bajo Mona, mouth of Quebrada Chiquero, along Río Caldera, alt. about 1500–2000 m., *Woodson, Allen & Seibert 1024*; humid forest around Los Siguas Camp, southern slope of Cerro de la Horqueta, alt. 1700 m., *Maxon 5539*; alt. 1700 m., *Pittier 3197, 5539*; Río Piarnasta Valley, 5 miles east of El Boquete, alt. 1525–1600 m., *Cornman 3534*; vicinity of El Boquete, alt. 1000–1300 m., *Maxon 5013*; Dexter Trail, El Boquete, *Killip 3534*.

The glabrous stems and leaves, shape, size and arrangement of the leaves, and rather long terminal peduncles characterize this species. No consistent difference has been noted by which *P. subquadrifolia* can be maintained as a distinct species.

13. PEPEROMIA QUATERNATA Miq. in Seem. Bot. Voy. Herald, 197. 1854.

A small, low, compactly and divaricately branched, succulent herb; stem sparingly hirsute; leaves in whorls of 4, round- or obovate-elliptic, rounded at both ends, scarcely 7 mm. wide × 10 mm. long, revolute, impressed-punctate, sparingly hirsute beneath, palmately 3-nerved; petiole 1–2 mm. long, retrorsely hispid; spikes terminal, closely flowered, scarcely 2 cm. long; peduncle 1 cm. long, hirsute; bracts round-peltate, golden- or red-glandular; rachis glabrous; fruit not known.

Panama and (?) adjacent South America.

CHIRIQUÍ: Volcano Chiriquí, *Seemann 895*.

14. PEPEROMIA CYCLOPHYLLA Miq. in Mart. Fl. Bras. 4^1:219. 1852, name only; Seemann, Bot. Voy. Herald, 198. 1854.

A small, repent, more or less crisp-pilose herb; stem about 1 mm. thick when dry, branching, internodes mostly 1–2 cm. long; leaves opposite, orbicular, mostly 5–10 mm. in diameter, occasional leaves 3–5 mm., pilose-pubescent on both sides, commonly slightly peltate, or the margin scarcely continuous over the petiole, loosely ciliate, drying coriaceous, subopaque, nerves scarcely evident or faintly palmately 3-nerved; petiole mostly about 1 mm. long, sparsely crisp-pubescent; spikes terminal or axillary, 1 mm. thick × 3–6 cm. long; peduncle 2-bracteate at or above the middle, crisp-pubescent, bracts linear or spatulate, pubescent; floral bracts round-peltate; fruit ovoid, pointed, stigma terminal.

Costa Rica and Panama. Also, in closely related forms, in the West Indies and South America.

PANAMA: without locality, *Seemann 607*. CHIRIQUÍ: forests around Puerto Remedios, alt. 0–30 m., *Pittier 3381*. VERAGUAS: trail between Cañazas and the foot of the Cordillera Central, headwaters of Río Cañazas, alt. 300–600 m., *Allen 140*. CANAL ZONE: western slope of Ancón Hill, vicinity of Balboa, alt. 20–75 m., *Seibert 123*; vicinity of Gatuncillo, *Piper 5652*; Río Pedro Miguel, near East Paraíso, *Standley 20087*. PANAMÁ: second growth, near Pacora River, *Miller 1775*; near big swamp east of Río Tecumen, *Standley 26542*; Río Tapia, *Standley 26195, 30670*; between Matías Hernández and Juan Díaz, *Standley 31038*; Chorrera, *Killip 3408*; swamp between El Jagua Hunting Club on Río Jagua and El Congor Hill, alt. 2 m., *Hunter & Allen 487*. DARIÉN: trail between Pinogana and Yavisa, alt. about 15 m., *Allen 252*.

15. PEPEROMIA QUADRANGULARIS (Thomps.) A. Dietr. Sp. Pl. 1:169. 1831.

Piper quadrangulare Thomps. in Trans. Linn. Soc. 9:202, *pl. 21, f. 1.* 1808.
Peperomia angulata H.B.K. Nov. Gen. & Sp. 1:66. 1815.
Piper angulatum Poir. in Lam. Encycl. Meth. 4:Suppl. 468. 1816.
Piper quadrangulum Willd. herb. fide Miq. Syst. Pip. 180. 1843.
Peperomia angulata var. *orbicans* Dahlst. in Kgl. Sv. Vet.-Akad. Handl. 33^2:157. 1900.
Peperomia Carlo-Wrightii Trel. in Fedde Rep. Sp. Nov. 23:23. 1926.
Peperomia Alleni Trel. in Ann. Mo. Bot. Gard. 25:825. 1938.
Peperomia saginans Trel. in Badillo in Cat. Fl. Venez. 1:246. 1945, nomen nudum.

A comparatively small, repent herb, epiphytic or on rocks; stem quadrangular, 1–2 mm. thick, minutely hirtellous to glabrate; leaves opposite, or occasionally roots replacing one of the leaves, rarely ternate, elliptic, obovate, or orbicular, 10–22 mm. wide × 12–30 mm. long, apex obtuse or very slightly pointed, base acute to rounded, palmately 3-nerved, nerves impressed above and more or less salient beneath, drying coriaceous and subopaque, sparsely hirtellous or glabrate, more or less variegated when living; petiole 2–4 mm. long, hirtellous; spikes axillary or occasionally terminal, 2–3 cm. long; peduncles 2–4 cm. long, 2-bracteate near the middle, hirtellous; floral bracts round-peltate, glandular-dotted; fruit ovoid, stigma at the apex of a short, thick style.

West Indies, Panama, and northern South America.

DARIÉN: trail between Pinogana and Yavisa, alt. about 15 m., *Allen 262.*

The specimen on which *P. Alleni* was based is rather fragmentary. It agrees in all respects, so far as can be determined, however, with those taken to represent this species from northern South America and Cuba.

16. PEPEROMIA BOCASENSIS Trel. in Ann. Mo. Bot. Gard. 27:300. 1940.

A repent-assurgent, red-tinged, succulent, epiphytic herb; stems about 2 mm. thick and sulcate when dry, internodes 2–7 cm. long, crisp-hirtellous; leaves in whorls of 3–4, elliptic, apex constricted, obtuse, base subobtuse or acute, 1–2 cm. wide × 1.5–3.5 cm. long, mostly about 1.5 × 2.5 cm., palmately 3-nerved, crisp-hirtellous above, especially along the nerves, glabrous beneath, ciliolate toward the apex, punctate, drying coriaceous, glossy, opaque; petiole hirtellous, channeled; spikes axillary and (?) terminal, 1 mm. thick × 7–11 cm. long, closely flowered; peduncle 4–5 cm. long, hirtellous; rachis with inter-ovary, anastomosing ridges; bracts round-peltate; fruit subglobose, about 1 mm. long, obliquely pointed into a stoutish style, stigma terminal.

Known only from Bocas del Toro.

BOCAS DEL TORO: vicinity of Nievecita, stem and peduncles deep red, alt. about 0–50 m., *Woodson, Allen & Seibert 1859.*

The hirtellous stems and upper surface of the blades, long spikes, and long peduncles distinguish this species.

17. Peperomia martagonifolia C.DC. in Ann. Conserv. & Jard. Bot. Genève 21:262. 1920, name only; in Candollea 1:313. 1923; Schroeder in Candollea 3:128. 1926.

An erect, somewhat branched or simple, essentially glabrous, fleshy, terrestrial, or epiphytic herb; stem up to 4 mm. thick below when dry, internodes commonly 3–4 cm. long above, the lowermost 15 cm., drying strongly ridged; leaves mostly 3–4 at a node, lance-elliptic, apex sharply long-acuminate, base acute-decurrent, 2–3.5 cm. wide × 5–9 cm. long, palmately 5-nerved, the midrib and innermost pair of nerves prominent, the apex minutely hirtellous, drying dull green, submembranous, subrevolute, translucent; petiole 1–2 cm. long, glabrous, or sparsely microscopically hirtellous; spikes terminal and axillary, closely flowered, 2 mm. thick × 10–14 cm. long; peduncle mostly 8–15 mm. long, glabrous or microscopically hirtellous; rachis reticulately ridged between the flowers; bracts very small, round-peltate; fruit ovoid, obliquely pointed, about 1 mm. long, with basal pseudocupule, stigma apical.

Mountains of Costa Rica and northern Panama.

chiriquí: Cuesta de las Palmas, southern slope of Cerro de la Horqueta, alt. 1700–2100 m., *Pittier 3269;* Bajo Chorro, Boquete District, alt. 1800 m., *Davidson 199.*

The conspicuous nerves, hirtellous leaf apices, lengths of petioles and peduncles, small bracts, etc. distinguish this species from *P. Seemanniana* and other related forms.

18. Peperomia Seemanniana Miq. in Seem. Bot. Voy. Herald, 198, *pl. 37.* 1854.

A glabrous, branched, suberect, terrestrial herb; stem 3–4 mm. thick when dry, 15–30 cm. or more tall, internodes 2–3 cm. long above, much longer downward, drying ridged-sulcate; leaves commonly opposite, less frequently ternate, lance-elliptic, occasional leaves oblanceolate or suboblong, apex attenuately sharp-acuminate, base acute-decurrent, 2–3 cm. wide × 6–10 cm. long, palmately 5- to 7-nerved, drying coriaceous, glandular-dotted, opaque; petiole 5–10 mm. long, grooved above, stout; spikes terminal and axillary, commonly multiple, 2 mm. thick × 6–8 cm. long, densely flowered; peduncle mostly 1–2 cm. long; bracts ovate-oblong-peltate, contiguous or overlapping; fruit globose-ovoid, pointed, stigma apical.

Northern Panama.

chiriquí: vicinity of El Boquete, alt. 1000–1300 m., *Pittier 2921; Maxon 5037;* alt. 1400–1650 m., *Killip 3542;* Bajo Mono, Boquete District, alt. 1350 m., *Davidson 556;* Chiriquí Volcano, *Seemann 896.*

19. Peperomia viridispica Trel. in Contr. U. S. Nat. Herb. 26:44. 1927.

Peperomia angustata H.B.K. var. *santamartae* C.DC. in Candollea 1:306. 1923.
Peperomia viridispica var. *perejil* Trel. Contr. U. S. Nat. Herb. 26:44. 1927.
Peperomia sarcocarpa Trel. loc. cit. 1927.

A rather large, repent, pendent, glabrous, succulent, epiphytic herb; stem 3–5 mm. thick when dry × 30 cm. or more long, rooting at the lower nodes, drying

angular-sulcate, internodes mostly 3–6 cm. long, occasionally up to 10 cm.; leaves 2–4 at a node, more commonly opposite, subrhombically lance-elliptic, oblanceolate, or rounded, 1.5–4 cm. wide × 3–7 cm. long, apex attenuately acuminate, blunt, base acute or subcuneate, drying submembranous, translucent, palmately 3- to 5-nerved, if 5-nerved the outermost pair of laterals thin and obscure; petiole 5–10 mm. long; spikes terminal or occasionally axillary, commonly solitary, loosely flowered, 2–3 mm. thick × 8–15 cm. long or occasionally somewhat longer; peduncle 1–5 cm. long; bracts oblong-ovate-peltate; fruit globose-ovoid, about 1 mm. long, obliquely pointed, stigma apical.

Panama and Colombia.

COCLÉ: Penonomé and vicinity, alt. 15–300 m., *Williams 382*. CANAL ZONE: Balboa, *Standley 27117, 28550, 28568*; vicinity of former town Empire, Culebra Cut and vicinity, alt. 80 m., *Hunter & Allen 785*; on boulders in deep shade, *Allen 2028*. PANAMÁ: Taboga Island, *Macbride 2808*; *Standley 27893*; Tumba Muerto Road, near Panamá, *Standley 29827*; between Las Sabanas and Matías Hernández, *Standley 31873, 31893*; near Pacora River, *Miller 1776, 1777, 1778*; hills northeast of Hacienda La Joya, 50–300 m., *Dodge, Hunter, Steyermark & Allen 16902*.

No significant difference has been found by means of which the Panamanian specimens can be differentiated from those seen from Colombia. The distantly spaced flowers and usually more membranous (when dry) leaves distinguish it from *P. Seemanniana*.

III. KEY TO SPECIES WITH GLOBOSE-OVOID, SUBBASALLY ATTACHED FRUIT WITH OBLIQUE SOMEWHAT POINTED APEX AND SUBAPICAL STIGMA.

(Subgenus SPHAEROCARPIDIUM Dahlst.).

a. Leaves opposite or verticillate (lower stem leaves sometimes alternate).
  b. Stems minutely velvety hirtellous.
    c. Leaves 5 mm. or less wide, 3 times or more longer than wide.
      d. Leaves scarcely 2 mm. wide, linear-oblong ..... 20. P. APODA
      dd. Leaves 2–5 mm. wide.
        e. Leaves spatulate, much longer than wide ..... 21. P. GALIOIDES
        ee. Leaves elliptic, scarcely twice longer than wide ..... 37. P. ALBESCENS
    cc. Leaves wider and proportionately shorter ..... 22. P. PALMANA
  bb. Stem not hirtellous.
    c. Stems glabrous; leaves commonly alternate, subplinerved ..... 23. P. ALLAGOTACTA
    cc. Stems more or less hairy.
      d. Stems villous, at least toward the base.
        e. Leaves 4–7 mm. wide ..... 24. P. BIFRONS
        ee. Leaves 10–20 mm. wide ..... 25. P. VALLICULAE
      dd. Stems villous at the nodes only.
        e. Leaves mostly 3–4 at a node ..... 26. P. BARBINODIS
        ee. Leaves 2 or 1 at a node ..... 27. P. SEIBERTII
aa. Leaves alternate.
  b. Rachis conspicuously papillate, plants subcaulescent ..... 28. P. KILLIPI
  bb. Rachis not obviously papillate.
    c. Leaves scarcely 1 cm. long, or occasionally up to 2 cm., plants repent.
      d. Leaves 2–3 mm. wide, oblong-spatulate ..... 29. P. NIEVECITANA
    dd. Leaves mostly wider, rounded, elliptical, or lanceolate.
      e. Leaves or some of them 2–3 times longer than wide.
        f. Stem essentially glabrous or with only a few scattered hairs; leaves very variable in shape ..... 30. P. CHIRIQUIENSIS
        ff. Stem evidently hairy.
          g. Leaves elliptic-obovate, apex round-emarginate ..... 31. P. HYGROPHILOIDES
          gg. Leaves narrowly elliptic, apex acute ..... 32. P. CHRYSLERI

ee. Leaves mostly scarcely twice as long as wide.
f. Spikes scarcely 5 mm. long..... 33. P. COCLEANA
ff. Spikes mostly 1–2 cm. or more long.
g. Leaves, or some of them, elliptic or lance-elliptic, subacute.
h. Stems villous..... 34. P. CRUENTATA
hh. Stems minutely hirtellous..... 35. P. TENUICAULIS
gg. Leaves mostly round, elliptic, or subobovate, obtuse.
h. Plants long-repent, leaves all alternate..... 36. P. ROTUNDIFOLIA
hh. Plants subcespitose, leaves congested 2–3 together above..... 37. P. ALBESCENS
cc. Leaves usually much larger.
d. Leaves conspicuously black-dotted.
e. Leaves elliptic-lanceolate, or ovate, mostly broader at or below the middle..... 38. P. GLABELLA
ee. Leaves elliptic-oblanceolate, mostly wider above the middle.
f. Leaves hairy on both sides; spikes about 15 cm. long..... 39. P. FLAGELLISPICA
ff. Leaves glabrous; spikes shorter..... 40. P. PERCUNEATA
dd. Leaves not obviously black-dotted though sometimes dark-glandular.
e. Stems glabrous (or somewhat pilose at the nodes only).
f. Inner nerves coalescing within the lowermost 5–10 mm.; leaves more or less elliptic-oblanceolate.
g. Spikes 3 cm. or more long..... 41. P. DIRUPTORUM
gg. Spikes 1 cm. long; peduncle equilong..... 23. P. ALLAGOTACTA
ff. Nerves not obviously coalescent.
g. Leaves 2.3–4.5 cm. wide.
h. Plants ascending scarcely 20 cm.; leaves abruptly and bluntly short-acuminate, nervules by transmitted light numerous and anastomosing..... 42. P. PASCUICOLA
hh. Plants to 1 m. tall; leaves, at least above, narrowly attenuately sharp-acuminate, nervules not conspicuously numerous or strongly anastomosing..... 43. P. ELATA
gg. Leaves mostly 2 cm. or less wide.
i. Leaves less than twice as long as wide..... 44. P. LEUCOSTICTA
ii. Leaves 2–3 times longer than wide.
j. Nodes more or less pilose; upper leaves opposite..... 27. P. SEIBERTII
jj. Nodes glabrous; upper leaves alternate..... 45. P. PARIETARIAEFOLIA
ee. Stems hairy.
f. Leaves mostly less than 2 cm. wide.
g. Plants ascending 10–15 cm.; stems villous upward..... 46. P. OBSCURIFOLIA
gg. Plants ascending to 30 cm. or more; stems villous downward, glabrescent above..... 25. P. VALLICULAE
ff. Leaves mostly 2–3.5 cm. wide, obtuse..... 47. P. DAVIDSONII

20. PEPEROMIA APODA Trel. in Contr. U. S. Nat. Herb. 26:44. 1927.

A small, stoloniferous herb; stem 2 mm. thick below when dry, rooting at the lower nodes; branches 1 mm. thick, ascending 5–8 cm., densely velvety-hirtellous; internodes mostly less than 1 cm. long; leaves mostly 4 at a node, oblong, apex rounded, sometimes emarginulate with bristle-like hairs, base acute, 2 mm. wide × 10 mm. long, glabrous on both sides or sparsely hirtellous near the base above, ciliolate near the base, 1-nerved, conspicuously yellow-glandular-dotted, drying firm, opaque; petiole about 0.5 mm. long, flat, hirtellous, marginally ciliolate; spikes terminal (?) and axillary, slender, 1 mm. thick × 4 cm. long, moderately flowered; peduncle 1–2 mm. long; bracts comparatively large, round-peltate, yellow-glandular-dotted; fruit ovoid, about 0.6 mm. long, apex rather acutely and obliquely pointed, stigma subapical.

Río Caldera valley, Chiriquí.

CHIRIQUÍ: valley of the Río Caldera, from El Boquete to the Cordillera, alt. 1400–1600 m., *Killip 3514*.

The densely hirtellous stems, whorled, narrowly oblong, glandular-dotted leaves, and obliquely, rather sharp-pointed fruits distinguish this species.

21. PEPEROMIA GALIOIDES H.B.K. Nov. Gen. & Sp. 1:71, *pl. 17*. 1815.

Piper galioides Poir. in Lam. Encycl. Meth. 4:Suppl. 470. 1816.
Peperomia suaveolens Ham. Prodr. Pl. Ind. Occ. 2: 1825, fide C.DC.
?*Peperomia Mollugo* Willd. in Miq. Syst. Pip. 156. 1843, as synonym.
Peperomia flagelliformis Hook. f. ex Miq. in Hook. Lond. Jour. Bot. 4:423. 1845.
Peperomia Jamesoni Regel in Bull. Soc. Nat. Moscou 31^2:544. 1858.
Peperomia agapatensis C.DC. in DC. Prodr. 16^1:455. 1869.
Peperomia galioides var. *longifolia* C.DC. loc. cit. 464. 1869.
Peperomia galioides var. *nigro-punctulata* C.DC. loc. cit. 1869.
Peperomia galioides var. *umbrosa* Henschen in Nov. Act. Soc. Sci. Upsal. III, 8:37. 1873.
Peperomia galioides var. *aprica* Henschen, loc. cit. 1873.
Peperomia subcorymbosa Sodiro, Contr. Conoc. Fl. Ecuator. Monogr. 1. ed. 2. 181. [1901].
Peperomia galioides var. *minutifolia* C.DC. in Ann. Conserv. & Jard. Bot. Genève 21:262. 1920.
Peperomia granata Trel. in Fedde Rep. Sp. Nov. 23:24. 1926.

A suberect, branched, succulent, epiphytic or terrestrial herb; stem 2–3 or rarely 8 mm. thick, up to 100 cm. long but mostly much shorter, branching di- or trichotomous or verticillate, the branches often slender, wand-like, and commonly rather strongly divergent, moderately to densely hirtellous; leaves 3–9 at a node, commonly 4–5, elliptic, elliptic-oblong, subspatulate, or oblanceolate, 2–5 mm. wide × 5–30 mm. long, apex obtuse, base acute, obscurely palmately 3-nerved or subplinerved, the midrib faintly branched upward, commonly more or less puberulent along the midrib at least near the base above and sometimes slightly so beneath, ciliolate toward the apex, often glandular-dotted, drying membranous; petiole very short, hirtellous; spikes terminal and axillary, solitary or in verticels of 3–6 spikes, 4–7 or rarely up to 15 cm. long; peduncle mostly about 5 or occasionally up to 10 mm. long, glabrate or sparsely hirtellous; bracts round-peltate; fruit about 1 mm. long, globose-ovoid, apex oblique, stigma subapical.

Nearly throughout the range of the genus in the Americas and the West Indies.

CHIRIQUÍ: Chiriquí Volcano, alt. 2450 m., *Killip 3585*.

This species does not appear to be common in Panama. The only specimen seen comes from the heights on Chiriquí Volcano. This specimen has leaves slightly more hirtellous than is common for the South American specimens and it appears more dingy when dry and with the leaves slightly more opaque. No other characters of any significance have been observed, however, by which it can de distinguished from this species.

22. PEPEROMIA PALMANA C.DC. in Bull. Soc. Bot. Belg. 29^2:71. 1890; 30^1:233. 1891.

Peperomia palmana var. *glabrior* C.DC. in Candollea 1:304. 1923.
Peperomia glabrior Trel. in Contr. U. S. Nat. Herb. 26:44. 1927.
Peperomia laesa Trel. in Ann. Mo. Bot. Gard. 27:402. 1940.

An erect or subassurgent, freely branching, terrestrial or epiphytic herb; stem 2–3 mm. thick toward the base when dry, up to 20–30 cm. tall, rooting from the lowermost nodes, moderately to densely velvety-hirtellous, internodes 3–5 cm. long below, reduced upward; leaves 2, 3, or 4 at a node, rather variable in size and shape, often on the same plant, elliptic, lance-elliptic, suborbicular or obovate, apex bluntly acuminate, base acute, 0.8–2.0 cm. wide × 1–5 cm. long, commonly 1–1.5 × 3–4 cm., very obscurely hirtellous on one or both sides, glabrescent, ciliolate toward the apex, distinctly palmately 3-nerved or the broader leaves 5-nerved, drying thin and translucent, glandular-dotted, somewhat pellucid-dotted; petiole up to 15 mm. long, mostly 5–10 mm., velvety-hirtellous; spikes axillary, 1–2 mm. thick × 2–6 cm. long, closely flowered; peduncle slender, hirtellous glabrescent; bracts round-peltate, rather conspicuously dark-glandular-dotted; fruit subglobose, about 0.5 mm. long, apex oblique, stigma subapical.

Costa Rica and western Panama.

CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, alt. about 1500–2000 m., *Woodson, Allen & Seibert 876, 971*; vicinity of "New Switzerland," central valley of Río Chiriquí Viejo, alt. 1800–2000 m., *Allen 1422*; valley of the Upper Río Chiriquí Viejo, vicinity of Monte Lirio, alt. 1300–1900 m., *Seibert 144, 140*; Boquete District, Bajo Chorro, alt. 1800 m., *Davidson 178*; above El Boquete, alt. 1400–1500 m., *Killip 3519*; vicinity of El Boquete, alt. 1000–1500 m., *Cornman 2052*; between the Río Ladrillo and Los Siguas Camp, southern slope of Cerro de la Horqueta, alt. 1200–1700 m., *Maxon 5401, 5541, 5553*; Cuesta de la Palmas, southern slope of Cerro de la Horqueta, alt. 1700–2100 m., *Pittier 3217*.

In the original description of this species DeCandolle said that the leaves and young stems were slightly puberulous, while he described variety *glabrior* in the Clavis as having glabrous stems. Trelease, later, in raising var. *glabrior* to specific status, likewise claimed that the plants representing the variety were glabrous. He also described *P. laesa* as glabrous. The type specimen of var. *glabrior* has definitely hirtellous stems and some of the leaves are likewise obscurely hirtellous. The type of *P. laesa* also shows the same characters. The leaves on the type of var. *glabrior* are somewhat larger than is common for other specimens cited here but this character is so variable that it does not appear advisable to use it for varietal distinction.

23. PEPEROMIA ALLAGOTACTA C.DC. in Candollea 1:317, 378. 1923.

A rather small, erect, fleshy, glabrous herb; stem 3–4 mm. thick when dry, 20 cm. or more tall, branched upward, the branches slender, divergent, internodes about 1 cm. long, those of the branches somewhat longer, drying wrinkled and subglossy; leaves alternate, those of the branches appearing opposite because of congestion, elliptic, elliptic-lanceolate, or suboblanceolate, apex somewhat narrowed but obtuse, base acute, 7 mm. wide × 2 cm. long, or those on the main stem 1.5× 4.5 cm., 5-plinerved, the laterals coalescing with the midrib near the base, the midrib branched upward, ciliolate toward the apex, glandular-dotted, drying membranous, translucent, paler beneath; petioles 2–5 mm. long, grooved above; spikes terminal, closely flowered, 1 mm. thick × 1 cm. long; peduncle about as

long as the spike; bracts round-peltate, about 0.5 mm. wide, glandular-dotted; ovary ovoid, apex oblique, stigma subapical; matured fruit not present.

Chiriquí Volcano.

CHIRIQUÍ: around El Potrero Camp, Chiriquí Volcano, alt. 2800–3000 m., *Pittier 3108*.

The plinerved leaves, congested and simulating an opposite or whorled arrangement on the branches, and short spikes characterize this species.

24. PEPEROMIA BIFRONS Trel. in Ann. Mo. Bot. Gard. 27:300. 1940.

A medium-sized, assurgent herb, branching from the base, simple above; stem 3–4 mm. thick when dry, rather densely villous when young, becoming glabrous above in older stems, drying sulcate and somewhat glossy, internodes mostly 1–3 cm. long; leaves mostly 3 or 4 at a node, oblong-elliptic or suboblanceolate, apex obtuse or submarginulate, base cuneate, 4–7 mm. wide × 1.5–3 cm. long, glabrous on both sides, ciliate toward the apex, obscurely palmately 3-nerved, drying rather firm, opaque, glandular-dotted beneath; petioles 2–5 mm. long, glabrous, flattened above, clasping-decurrent; spikes terminal and axillary, 2 mm. thick × 3.5 cm. long, rather closely flowered; peduncle comparatively thick, 1–2 cm. long, glabrous; bracts round-peltate; ovary ovoid, apex oblique, stigma subapical; mature fruit not present.

Known only from one locality in Chiriquí.

CHIRIQUÍ: Finca Lerída to Boquete, alt. about 1300–1700 m., *Woodson, Allen & Seibert 1132*.

25. PEPEROMIA VALLICULAE Trel. in Ann. Mo. Bot. Gard. 24:186. 1937.

A rather large, assurgent herb; stem 3–5 mm. thick below when dry, ascending to 30 cm. or more, villous toward the base, glabrescent upward, internodes 3–4 cm. long below, reduced upward; leaves alternate or sometimes 2 or 3 at a node, subrhombically oblanceolate, apex blunt, emarginulate, base cuneate, 1–2 cm. wide × 2.5–5 cm. long, rather obscurely palmately 3-nerved, glabrous on both sides, ciliolate toward the apex, dark-glandular-dotted, drying firm and opaque, paler beneath; petiole 5–10 mm. long, grooved above, glabrous, clasping-decurrent; spikes terminal and axillary, 1 mm. thick × 10–18 cm. long, closely flowered; peduncles 1–2 cm. long, glabrous; bracts round-peltate, glandular-dotted; fruit ovoid, about 0.5 mm. long, apex oblique, stigma subapical.

Known only from Cerro Valle Chiquito, Coclé.

COCLÉ: western slope and summit of Cerro Valle Chiquito, alt. 700–800 m., *Seibert 503*.

The stems villous downward, alternate-opposite-whorled, oblanceolate leaves, and long spikes are distinguishing characters of this species.

26. PEPEROMIA BARBINODIS Trel. in Contr. U. S. Nat. Herb. 26:200. 1929.

Peperomia chiqueroana Trel. in Ann. Mo. Bot. Gard. 27:301. 1940.

A rather large, erect, openly branching herb; stem 3–4 mm. thick below when dry, up to 30 cm. or more tall, glabrous except for the prominently villous nodes,

internodes 10 cm. long below, somewhat shorter upward; leaves 2, 3, or 4 at a node, elliptic, elliptic-lanceolate, or suboblanceolate, apex acuminate, base acute, 1–2 cm. wide × 3.5–6 cm. long, glabrous and paler beneath, the nerves above crisp-pubescent, densely ciliolate toward the apex, 5-nerved, the midrib and innermost pair of lateral nerves prominent, the outermost pair inconspicuous, coalescing near the base, drying membranous, translucent, faintly glandular-dotted; petiole about 5 mm. long, glabrous, grooved above; spikes terminal and axillary, loosely flowered, very slender, 6 cm. long; peduncle about 1 cm. long, glabrous; bracts round-peltate; ovary ovoid, apex oblique, stigma subapical.

Costa Rica and western Panama.

CHIRIQUÍ: Bajo Mona, mouth of Quebrada Chiquero, along Río Caldera, alt. about 1500–2000 m., *Woodson, Allen & Seibert 1025*.

The type, *Tonduz 10419*, from Costa Rica, has leaves smaller than the Panamanian collection cited above, but otherwise the specimens appear to be nearly identical.

27. PEPEROMIA SEIBERTII Trel. in Ann. Mo. Bot. Gard. 24:185. 1937.

A moderately large, openly branched, essentially glabrous herb, drying yellow; stem 3 mm. thick below when dry, up to 30 cm. or more tall, somewhat villous at the nodes, internodes up to 10 cm. long below, reduced upward; leaves both alternate and opposite, broadly lanceolate, apex sharply acuminate, base acute, 1–2.5 cm. wide × 2.5–6 cm. long, palmately 3- to 5-nerved, the midrib and innermost pair of lateral nerves salient beneath, pale-glandular-dotted and glabrous beneath, pubescent at the base above, ciliate toward the apex, drying membranous, translucent; petiole scarcely 5 mm. long, grooved above, alately decurrent; spikes terminal and axillary, 1 mm. thick × 5–7 cm. long, loosely flowered; peduncle slender, 5–10 mm. long; bracts round-peltate; ovary ovoid, apex oblique, stigma subapical; fruit not present.

Near Monte Lirio, Chiriquí.

CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, alt. 1300–1900 m., *Seibert 201*.

The alternate-opposite leaf arrangement, leaves pubescent at the base above, and pilose nodes distinguish this species.

28. PEPEROMIA KILLIPI Trel. in Bot. Gaz. 73:143. 1922.

Peperomia hymenodes Trel. in Contr. U. S. Nat. Herb. 26:43. 1927.

A small, very short-stemmed herb; stem 3 mm. thick, subrhizomatous, ascending 2–3 cm., glabrous, internodes very short, drying wrinkled and scaly; leaves alternate, round- to elliptic-ovate, apex acute or obtusish, base cordate or cordulate, 1.5–3.5 cm. wide × 3–6 cm. long, sparsely appressed-pubescent above, glabrous beneath, rather densely ciliolate throughout, palmately 7-nerved, drying very thin, translucent, pale glandular-dotted; petioles very slender, commonly 3–5 cm. long, glabrous or sparsely pubescent along the groove, abruptly enlarging into a thick-

ened base which remains as part of the stem when the leaf falls off; spikes apparently axillary, 1 mm. thick × 5–9 cm. long, closely flowered; peduncles up to 5.5 cm. long, glabrous; rachis ridges conspicuously papillate; bracts round-peltate, granulate; fruit ovoid. scarcely 0.5 mm. long, apex oblique, stigma subapical.

Panama.

CHIRIQUÍ: eastern Chiriquí, vicinity of San Felix, alt. 0–120 m., *Pittier 5266.* CANAL ZONE: Río Paraíso, above East Paraíso, *Standley 29890;* Canal Zone and adjacent Panama, forest along small, unnamed quebrada entering lake at 70 m. level, alt. 70–80 m., Río Indio, *Dodge & Allen 17290;* sabanas along drowned Río Azote Caballo, alt. 66–70 m., *Dodge, Steyermark & Allen 16867;* near Madden Dam and along Azote Caballo Road near Alahuela, alt. 90–100 m., *Dodge 16587.* COLÓN: Alhajuela, Chagres River, *Killip 3218;* between Alhajuela and El Vigia, *Pittier 2369.* PANAMÁ: Río La Maestra, alt. 0–25 m., *Allen 38;* Perlas Archipelago, San José Island, *Johnston 443, 1138.*

The leaves on the type specimen are round-ovate with obtusish apex while those on the type of *P. hymenodes* are elliptic-ovate with acutish apex. Other specimens show intergrading shapes. The very short stem, long, slender petioles and peduncles, and especially the strongly papillate rachis are distinctive features. It resembles *P. hispidorhachis* in general but differs in its sparser pubescence, less hispid rachis, and the shape of the fruit.

29. PEPEROMIA NIEVECITANA Trel. in Ann. Mo. Bot. Gard. 27:304. 1940.

A small, matted, repent-assurgent epiphytic herb; stem scarcely 1 mm. thick, fertile branches up to 5 cm. tall, crisp-pubescent, internodes short; leaves alternate, oblong-spatulate, apex obtuse, base acutish, 2–3 mm. wide × 6–8 mm. long, glabrous, somewhat ciliolate toward the apex, glabrescent, glandular-dotted, inconspicuously 1-nerved, drying dark, opaque; petioles 1 mm. long, glabrous, flattened; spikes terminal, scarcely 1 mm. thick × 2–3 cm. long, moderately flowered; peduncle slender, about 5 mm. long, sparsely pubescent glabrescent; bracts round-peltate; fruit globose-ovoid, scarcely 0.5 mm. long, apex oblique, stigma subapical.

Vicinity of Nievecita, Bocas del Toro.

BOCAS DEL TORO: vicinity of Nievecita, alt. 0–50 m., *Woodson, Allen & Seibert 1865.*

The repent, pubescent stems, alternate, small, glabrous, spatulate leaves, and small fruits distinguish this species.

30. PEPEROMIA **chiriquiensis** Yuncker, sp. nov.

Herba parva repens stolonifera, caule filiformi glabro vel dissite pubescente; foliis alternis elliptico-subobovatis, ovato-oblongis vel lanceolato-oblongis, apice rotundatis, basi acutis, obscure palmatim 3-nerviis, glabris vel supra dissite pubescentibus, ciliatis; petiolo 2–4 mm. longo amplectenti-decurrente; spicis terminalibus et (?) axillaribus; pedunculo 5–10 mm. longo, glabro; drupa globosa, apice obliqua, stigmate subapicali.

A rather small, repent-stoloniferous herb; stem scarcely 1 mm. thick, branching, fruiting branches ascending to 5 cm., rooting from the nodes, essentially glabrous, with a few widely scattered hairs, internodes about 2 cm. long, reduced on the fruiting branches; leaves alternate, very variable in size and shape, those on the

stolons elliptic-subobovate, 4–7 mm. wide × 5–10 mm. long, apex rounded, base acute, those on the erect shoots becoming ovate- or lance-oblong and up to 1.5–2 cm. long, rather obscurely palmately 3-nerved, the midrib impressed above, glabrous or sparsely pilose above, paler and glandular-dotted beneath, ciliate especially above the middle, drying rather thin, translucent; petiole 2–4 mm. long, clasping-decurrent; spikes terminal and (?) axillary, 1 mm. thick × 3–4 cm. long, rather loosely flowered; peduncle 5–10 mm. long, glabrous; bracts round-peltate; fruit globose, eventually on pseudopedicels, apex oblique, stigma subapical.

Known only from the type locality.

CHIRIQUÍ: humid forest above Camp I, Holcomb's Trail, above El Boquete, alt. 1800–2100 m., Feb. 18, 1918, *Killip 3564* (U. S. Nat. Herb., TYPE).

This species bears some resemblance to *P. Jamesoniana* of Ecuador and Colombia but differs in the shape of the non-emarginulate, glandular-dotted leaves.

31. PEPEROMIA HYGROPHILOIDES C.DC. in Candollea 1:329. 1923.

A small, repent, branching, epiphytic herb; stem 1 mm. thick, creeping on trees, crisp-pubescent, scurfy-exfoliating, internodes 1–2 cm. long, much reduced on the short, erect, fertile branches; leaves alternate or the very uppermost opposite, elliptic-obovate, apex rounded or emarginate, base acutish, 5–8 mm. wide × 8–13 mm. long, much reduced upward on fertile branches, crisp-puberulent above, glabrous and conspicuously brown-glandular-dotted beneath, ciliate toward the apex, obscurely palmately 3-nerved, the midrib faintly nerved upward, drying firm, subtranslucent; petiole 3–5 mm. long, filiform, glabrous or sparsely puberulent; spikes terminal on short axillary branches, 1 mm. thick × 2–2.5 cm. long, closely flowered; peduncle 5–8 mm. long, glabrous; bracts round-peltate; fruit globose, apex oblique, stigma subapical.

Southern slope of Cerro de la Horqueta, Chiriquí.

CHIRIQUÍ: southern slope of Cerro de la Horqueta, vicinity of Las Siguas Camp, alt. 1700 m., *Pittier 3203*.

This species is apparently closely related to *P. rotundifolia* from which it differs because of the type of pubescence and the shape of the leaves.

32. PEPEROMIA **Chrysleri** Yuncker, sp. nov.

Herba parva stolonifera, ramis fructiferis ad 5 cm. adscendentibus dissite villosis; foliis alternis, oblongo-ellipticis, utrinque acutis, utrinque glabris, apicem versus ciliolatis; petiolo 2–3 mm. longo, villoso; spicis terminalibus; pedunculo 1 cm. longo, crispe-pubescente; ovario obovoideo, apice obliqua, stigmate subapicali.

A small, stoloniferous herb; stem 1 mm. thick, fertile branches ascending to 5 cm., loosely villous, internodes about 1 cm. long; leaves alternate, elliptic-oblong, acute at both ends, about 5 mm. wide × 15–20 mm. long, 1-nerved, glabrous on both sides or with a few hairs near the base above, ciliolate toward the apex, paler and pale-glandular-dotted beneath, drying subcoriaceous and subopaque; petiole

2–3 mm. long, villous; spikes terminal, 1 mm. thick × 7 cm. long, moderately flowered; peduncle about 1 cm. long, crisp-pubescent; bracts round-peltate; ovary obovoid, apex oblique, stigma subapical; fruit not matured.

Known only from the type locality.

CANAL ZONE: Barro Colorado Island, June 29, 1940, *M. A. Chrysler 4797* (Herb. Univ. Ill., TYPE).

The small plants with villous stems, and leaf shape distinguish this species.

33. PEPEROMIA COCLEANA Trel. in Ann. Mo. Bot. Gard. 25:826. 1938.

A small, repent herb; stem less than 1 mm. thick, glabrous, branching, the fruiting branches 1–2 cm. long, internodes mostly less than 1 cm. long; leaves alternate, round, apex obtuse, base acutish, scarcely 5 mm. wide, loosely pilose above, glabrous beneath, ciliate, faintly 1-nerved, drying thickish, subtranslucent, apparently fleshy when living; petiole 1–2 mm. long, glabrous; spikes 1 mm. thick × 2–4 mm. long, densely flowered, terminal and axillary on short, axillary branches; peduncle scarcely 5 mm. long, glabrous; bracts round-peltate; fruit subdepressed-globose, scarcely 0.5 mm. long, apex bluntly and slightly oblique, stigma nearly apical.

Upper Río Mata Ahogado valley, Coclé.

COCLÉ: valley of the upper Río Mata Ahogado, alt. 350 m., *Allen 133*.

The small, round leaves, glabrous filiform stem, and especially the very small spikes, distinguish this species from *P. rotundifolia* which it superficially resembles.

34. PEPEROMIA CRUENTATA Trel. in Ann. Mo. Bot. Gard. 27:302. 1940.

A small, repent herb; stem filiform, moderately to densely villous, branches up to 5 cm. tall; internodes up to 1 cm. long; leaves alternate, crimson between the veins when fresh, round or subobovate, apex rounded, base acutish, those on the branches elliptic or lance-elliptic, acute at both ends, the rounded lower leaves about 5 mm. in diameter, the upper leaves 3–5 mm. wide × 8–14 mm. long, palmately 3-nerved, glabrous on both sides or with occasional hairs above, rather strongly ciliate, drying membranous, translucent, inconspicuously glandular-dotted; petiole 1–2 mm. long, grooved above, more or less hairy; spikes terminal on short, erect, few-leaved shoots, 1 mm. thick × 3–4 cm. long, rather closely flowered; peduncle about 5 mm. long, villous, the hairs extending on the rachis above the lowermost several flowers; bracts round-peltate, densely glandular-dotted; fruit scarcely 0.5 mm. long, globose, apex oblique, stigma subapical.

Isla de Colón, Bocas del Toro.

BOCAS DEL TORO: Isla de Colón, alt. 25–75 m., *Woodson, Allen & Seibert 1941*.

Trelease cited *Woodson, Allen & Seibert 1938* first when he originally described this species. The specimen in the Missouri Botanical Garden Herbarium of this number, which would presumably be taken as the type, is rather meagre and does not show the characters of the species as given in the description. It appears to be more properly a specimen of *P. rotundifolia* to which it is now being referred. The

above description is drawn from *No. 1941* of the same collectors, and the specimen in the Missouri Botanical Garden as sheet *No. 1170515* is taken to be the type. The label on this specimen gives the data as cited above. A specimen, obviously of the same collection and carrying the same number in the New York Botanical Garden Herbarium gives the location as Río Cricamola, between Finca St. Louis and Konkintoë, Bocas del Toro, alt. 10–50 m., Aug. 12–16, 1938.

The villous plants, elliptic leaves, and rachis pubescent toward the base distinguish this species from *P. rotundifolia* with which it is obviously related.

35. Peperomia tenuicaulis C.DC. in Anal. Inst. Fis.-Geogr. Costa Rica 9:177. 1897.

A slender-stemmed, repent herb; stem filiform, less than 1 mm. thick, branching, minutely hirtellous, internodes mostly about 1–1.5 cm. long; leaves alternate, ovate-elliptic, apex acute or obtuse, base subpeltate with the margin barely continuous over the petiole, or acutish, palmately 3-nerved, the nerves slender, puberulent on both sides, ciliolate near the apex, glandular-dotted, drying thin, translucent; petiole filiform, 1–2 mm. long, shallowly grooved above, minutely hirtellous; spikes terminal, 1 mm. thick × 3–5 cm. long, densely flowered; peduncle less than 5 mm. long, minutely hirtellous, with 2 small, lanceolate bracts near the middle, the bracts bristly at the apex; floral bracts round-peltate; fruit subglobose, about 0.6 mm. long, apex oblique, stigma subapical.

Costa Rica and Panama.

Canal Zone and adjacent Panama: drowned forest of quebrada below Río Indio Hydrographic Station, alt. 70 m., *Steyermark 17387*.

36. Peperomia rotundifolia (L.) H.B.K. Nov. Gen. & Sp. 1:65. 1815.

Piper rotundifolium L. Sp. Pl. 30. 1753.
Piper nummularifolium Sw. Prodr. Veg. Ind. Occ. 16. 1788.
Peperomia nummularifolia H.B.K. loc. cit. 66. 1815.
Acrocarpidium nummularifolium Miq. in Versl. en Medel. Kon. Nederl. Inst. 198, *pl. 2*. 1843.
?*Peperomia rotundifolia* f. *ovata* Dahlst. in Kgl. Sv. Vet.-Akad. Handl. 33^2:101. 1900.
Peperomia rotundifolia var. *subglabrilimba* C.DC. in Candollea 1:326. 1923.
Peperomia rotundifolia var. *subelliptica* Trel. in Fedde Rep. Sp. Nov. 23:18. 1926, nomen nudum.

A small, repent herb; stem filiform, scarcely 1 mm. thick, fruiting branches short, erect, moderately crisp-puberulent or somewhat villous glabrescent; leaves alternate, round, about 5 mm. in diameter, or round-elliptic or subobovate and up to 10 mm. wide × 12 mm. long, apex obtuse, base rounded-subpeltate with the lower margin scarcely continuous over the petiole, or sub-acute, moderately crisp-puberulent, loosely villous, or commonly glabrescent, more or less ciliate, obscurely palmately 3-nerved, often glandular-dotted, drying membranous; petiole commonly 1–5 mm. long, or occasionally up to 10 mm.; spikes solitary, scarcely 1 mm. thick × 2 cm. long, or occasionally somewhat longer, terminating short branches which commonly bear 1–3 or 4 leaves reduced in size upward; peduncle 3–5 mm. or rarely

up to 10 mm. long, crisp-puberulent or glabrate; bracts round-peltate; fruit about 0.8 mm. long, globose-ovoid, apex oblique, stigma subapical.

Throughout the American range of the genus in numerous scarcely distinguishable forms.

BOCAS DEL TORO: vicinity of Nievecita, alt. 0–50 m., *Woodson, Allen & Seibert 1847*; Isla de Colón, alt. 25–75 m., *Woodson, Allen & Seibert 1938*; Changuinola Valley, *Dunlap 455*; vicinity of Chiriquí Lagoon, *von Wedel 1137*. CHIRIQUÍ: valley of the Río Piarnasta, about 5 mi. east of El Boquete, alt. 1525–1600 m., *Killip 3537*; Boquete District, Chiquero, alt. 1650 m., *Davidson 510*. CANAL ZONE: near Río Medio, *Miller 1733, 1741*; Barro Colorado Island, alt. 120 m., *Standley 40901; Kenoyer 301*; Bohio, Soldado, *Cowell 225*; around Frijoles, alt. 25–30 m., *Pittier 3759*. COLÓN: Río Fató, alt. 10–100 m., *Pittier 3888*. DARIÉN: Caña-Cuasi Trail, Chepigana Distr., alt. 600 m., *Terry & Terry 1443*.

The variation in size and shape of the leaves is considerable on some specimens. The pubescence also is quite variable. Both crisp-puberulent and villous leaves may sometimes occur on the same plant.

37. PEPEROMIA ALBESCENS Trel. in Ann. Mo. Bot. Gard. 27:299. 1940.

A small, repent, subcespitose herb; stem 1 mm. thick, rooting at the nodes, erect branches up to 5 cm. tall, subretrorsely velvety-puberulent; internodes 1–2 cm. long below, shorter upward; leaves alternate or congested above and 2 or 3 together, broadly elliptic or subobovate, apex rounded, base acutish, 3–6 mm. wide × 5–10 mm. long, sparsely hirtellous glabrescent on both sides, bristly hairy at the apex, inconspicuously 1-nerved, drying firm, whitish, opaque; petiole 2–3 mm. long, subretrorsely puberulent; spikes terminal, often somewhat curved, 1 mm. thick × 10–15 mm. long, densely flowered; peduncle 5–10 mm. long, sparsely puberulent; bracts round-peltate; ovary ovoid, apex oblique, stigma subapical; mature fruit not present.

Coclé.

COCLÉ: vicinity of El Valle, alt. 600–1000 m., *Allen 1259*.

The small plants, small, elliptic, alternate-opposite-whorled leaves, and short spikes characterize this species. It is to be distinguished from *P. rotundifolia* because of the habit of growth, type of pubescence, crowded branch leaves, etc.

38. PEPEROMIA GLABELLA (Sw.) A. Dietr. Sp. Pl. 1:156. 1831.

Piper glabellum Sw. Prodr. Veg. Ind. Occ. 16. 1788.
Piper scandens Sw. loc. cit. 1788, not Vahl.
Peperomia brachyphylla A. Dietr. loc. cit. 157. 1831.
Peperomia caulibarbis Miq. Syst. Pip. 98. 1843.
Peperomia lineatipila A. Rich. in La Sagra, Fl. Cub. 11:229. 1850.
Peperomia trinervis Ruiz & Pav. var. *brachyphylla* C.DC. in DC. Prodr. 16^1:417. 1869.
Peperomia caulibarbis var. *brachyphylla* (A. Dietr.) Dahlst. Kgl. Sv. Vet.-Akad. Handl. 33^2:120. 1900.
Peperomia glabella var. *brachyphylla* (A. Dietr.) C.DC. in Urb. Symb. Ant. 3:236. 1902.
?*Peperomia chagalana* C.DC. in Engl. Bot. Jahrb. 40:259. 1908.
?*Peperomia sublaxiflora* C.DC. loc. cit. 262. 1908.

Peperomia similis Britt. in Mem. Torrey Bot. Club 16:61. 1920.
Peperomia cubana C.DC. f. *platana* Trel. in Fedde Rep. Sp. Nov. 23:19. 1926.
Peperomia lineatipila f. *mogotana* Trel. loc. cit. 1926.
Peperomia leucandra Trel. in Contr. U. S. Nat. Herb. 26:46. 1927.
Peperomia fusco-ciliata Trel. loc. cit. 1927.

A black-glandular-dotted, stoloniferous-assurgent herb; stem 1–2 mm. thick, branches ascending to 15 cm. or more, glabrous except for the ciliate petioles and lines decurrent from their margins below the nodes; leaves ovate to ovate-elliptic-lanceolate, 8–13 mm. wide × 15–35 mm. long, or occasionally up to 2.5 × 6 cm., acute to acuminate at both ends or not infrequently blunt or subobtuse, palmately 3- to 5-nerved, or plinerved within the lowermost 5–7 mm., ciliated near the apex, or some leaves throughout, mostly drying dark and subopaque; petiole 5–10 mm. long, grooved above, clasping-decurrent, mostly crisp-ciliate; spikes terminal and from the upper leaf axils, slender, up to 5–8 or occasionally as much as 12 cm. or more long; peduncle 10–15 mm. long; bracts round-peltate, black-dotted; fruit globose-ovoid, apex oblique, somewhat scutelliform and scutellum commonly with a thin margin, stigma subapical.

West Indies, Central America, and northern South America, in various scarcely distinguishable forms.

PANAMA: without locality, *Hayes 519*. CHIRIQUÍ: vicinity of San Felix, eastern Chiriquí, alt. 0–120 m., *Pittier 5143*. CANAL ZONE: valley of Masambí, on road to Las Cascadas Plantation, alt. 20–100 m., *Pittier 2593;* Las Cascadas Plantation, near Summit, *Standley 29652; Dodge & Hunter 8657;* near Río Medio, *Miller 1719, 1743;* Chico Trail, Río Indio, *Steyermark & Allen 17460;* near Salamanca Hydrographic Station on the gorge of the Río Pequení, 70–80 m. alt., *Dodge, Steyermark & Allen 16070;* near Madden Dam and along Azote Caballo Road near Alahuela, alt. 90–100 m., *Dodge 16588;* Barro Colorado Island, *Kenoyer 302*. COLÓN: forests around Porto Bello, alt. 5–100 m., *Pittier 2448*.

38a. PEPEROMIA GLABELLA var. **nervulosa** (C.DC.) Yuncker, comb. nov.

Micropiper melanostigma Miq. Comm. Phyt. 51. 1840.
Peperomia melanostigma Miq. Syst. Pip. 90. 1843.
Peperomia melanostigma var. *nervulosa* C.DC. in DC. Prodr. 16^1:409. 1869.
Peperomia glabella var. *melanostigma* Dahlst. in Kgl. Sv. Vet.-Akad. Handl. 33^2:122. 1900.
Peperomia conjungens Trel. in Contr. U. S. Nat. Herb. 26:45. 1927.

Plants mostly larger than in the typical form; leaves lanceolate or elliptic-lanceolate, apex acute to sharp-acuminate, base acute to cuneate, 1–3 cm. wide × 3–8 cm. long.

Found with the species.

CANAL ZONE: Las Cascadas Plantation, near Summit, *Standley 25730;* hills north of Frijoles, *Standley 27411;* Barro Colorado Island, *Standley 31343;* near Salamanca Hydrographic Station on the gorge of the Río Pequení, alt. 70–80 m., *Dodge, Steyermark & Allen 16982a*.

The densely black-dotted plants, ciliate petioles with decurrent subnodal ciliate lines, and leaf shape characterize this species. From *P. flagellispica* and *P. percuneata* it is to be distinguished chiefly because of the shape of the leaves.

39. PEPEROMIA FLAGELLISPICA Trel. in Field Mus. Nat. Hist. Bot. Ser. 18:314. 1937.

A moderate-sized, subrepent, conspicuously black-dotted (the dots are comparatively small), epiphytic herb; stem about 2 mm. thick, ascending to 10 cm. or more, sparsely pilose, especially near the nodes, internodes 1.5–4 cm. long; leaves alternate, elliptic-oblanceolate, apex gradually sharp-acuminate, base cuneate, loosely pilose on both sides, bristly hairy at the apex, 1.5–2 cm. wide × 4–6 cm. long, palmately 5-nerved, the innermost pair of lateral nerves confluent with the midrib near the base, drying firm, subopaque; petiole 5–10 mm. long, ciliate, clasping-decurrent; spikes terminal and axillary, solitary or commonly paired on a short stalk, 1 mm. thick × 12–16 cm. long, rather loosely flowered; peduncle 1–1.5 cm. long, glabrous; bracts round-peltate, black-dotted; fruit ovoid, about 0.8 mm. long, apex obliquely rather acutely pointed, stigma subapical.

Changuinola Valley, Bocas del Toro.

BOCAS DEL TORO: Farm 1, Changuinola Valley, *Dunlap 453*.

This species resembles *P. glabella* in its dark dotting and ciliate petioles but differs because of the leaf shape and pubescence, and spike characters.

40. PEPEROMIA PERCUNEATA Trel. in Contr. U. S. Nat. Herb. 26:46. 1927.

A moderately small, stoloniferous, black-dotted herb; stem 1–2 mm. thick when dry, rooting at the nodes, fertile branches ascending to 5–10 cm., more or less ciliate below the petiole margins, internodes 2–4 cm. long; leaves alternate, rhombic- or elliptic-oblanceolate, apex acuminate, base cuneate, glabrous on both sides, ciliolate toward the apex, 8–15 mm. wide × 3–5.5 cm. long, palmately 5-nerved, the lateral nerves obscure, drying firm, subopaque; petiole 3–5 mm. long, channelled above, margins ciliate, clasping-decurrent; spikes terminal and axillary, moderately flowered, 1 mm. thick × 10 cm. long; peduncle 5–10 mm. long, glabrous; bracts round-peltate, black-dotted; ovary ovoid, apex oblique, stigma subapical.

Panama.

CHIRIQUÍ: along Río Dupí, near sea-level, *Pittier 5224*. COLÓN: along Río Fató, in forests or thickets, alt. 10–100 m., *Pittier 3914*.

This species resembles *P. glabella* to a considerable extent but differs primarily because of the leaf shape. It differs from *P. flagellispica*, which it also resembles somewhat, because of its glabrous leaves.

41. PEPEROMIA DIRUPTORUM Trel. in Ann. Mo. Bot. Gard. 27:302. 1940.

A moderately small, glabrous, rhizomatous herb; stem 2 mm. thick when dry, branches ascending to 15 cm. or more, internodes 1–2 cm. long; leaves alternate, elliptic-oblanceolate or subobovate, lower leaves subspatulate, apex acute or lower leaves very obtuse, base acute to cuneate, 1–2.5 × 2–5 cm., 5-nerved with the innermost lateral nerves coalescing with the midrib within the lowermost 5–10 mm., bristly-hairy at the apex, drying moderately thin, subtranslucent, paler

beneath; petioles 5–8 mm. long, channelled above and narrowly winged by the decurrent blade, clasping-decurrent; spikes terminal, as yet immature, 2 mm. thick × 3.5 cm. long, densely flowered; peduncle 1 cm. long; bracts round-peltate, glandular-dotted; ovary ovoid, apex oblique, stigma subapical.

Bajo Mona, Chiriquí.

CHIRIQUÍ: Bajo Mona, mouth of Quebrada Chiquero, along Río Caldera, alt. 1500–2000 m., *Woodson, Allen & Seibert 1023*.

42. PEPEROMIA PASCUICOLA C.DC. in Candollea 1:352. 1923.

Peperomia novae-helvetiae Trel. in Ann. Mo. Bot. Gard. 27:304. 1940.
Peperomia rivi-vetusi Trel. loc. cit. 1940.

A medium-sized, assurgent, glabrous herb; stem 3–4 mm. thick when dry, ascending to 20 cm., internodes mostly 1–3 cm. long; leaves alternate, broadly lance-elliptic or subobovate, 2–3.5 cm. wide × 4–8 cm. long, apex rather abruptly acuminate, or occasional leaves obtuse, base acute, palmately 5-nerved, rather densely venulose by transmitted light, the nervules anastomosing, apex somewhat bristly-hairy, drying thin, translucent; petiole mostly about 1 cm. long, clasping-decurrent; spikes axillary and terminal, 2 mm. thick × 6–9 cm. long, rather closely flowered; peduncle about as long as the petiole; bracts round-peltate; fruit about 0.8 mm. long, subglobose or somewhat flattened laterally, at first subimmersed, eventually exserted on pseudopedicels, apex obliquely short-rostellate, stigma subapical.

Southwestern Panama.

CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, alt. 1300–1900 m., *Seibert 136*; vicinity of "New Switzerland," central valley of Río Chiriquí Viejo, alt. 1800–2000 m., *Allen 1360, 1417*; El Boquete, alt. 1400–1650 m., *Killip 3547*; alt. 1000–1300 m., *Pittier 2913*.

43. PEPEROMIA ELATA C.DC. in Candollea 1:355. 1923.

A rather large, divaricately branching, tree-like, glabrous herb; stem "about 1 m. tall, green, conspicuously mottled with red," internodes 6 cm. or more long below, reduced upward; leaves alternate, lance-elliptic and rather long-acuminate, or lower leaves round-elliptic and abruptly and bluntly short-acuminate, base acute, 2–3 cm. wide × 6–7 cm. long, or lower leaves 4–5 × 6–7 cm., ciliate toward the apex, palmately 5- or faintly 7-nerved, the nerves prominent, drying thin, translucent, rather densely glandular-dotted, "very dark, lustrous and satiny above; below very pale, non-lustrous and conspicuously ribbed" when living; petiole mostly 5–10 mm. long, grooved above, clasping-decurrent; spikes axillary and terminal, "dark red" when living, 2 mm. thick × 6–10 cm. long, moderately flowered; peduncle about 1 cm. long; bracts round-peltate; ovary obovoid, apex oblique, stigma subapical; fruit not matured.

Above El Boquete, Chiriquí.

CHIRIQUÍ: humid forest along the upper Caldera River, near "Camp 1", Holcomb's Trail, above El Boquete, alt. 1450–1650 m., *Maxon 5582*.

This species is similar to *P. portobellensis* in many respects, from which it differs, however, because of its axillary rather than sympodial spikes.

44. PEPEROMIA LEUCOSTICTA Trel. in Contr. U. S. Nat. Herb. 26:46. 1927.

Peperomia appellator Trel. in Ann. Mo. Bot. Gard. 27:300. 1940.
Peperomia simulatio Trel. loc. cit. 305. 1940.

A rather small, repent-assurgent, glabrous, mountain herb; stem about 2 mm. thick, fertile branches ascending to 10–15 cm., internodes 1–2 cm. long; leaves alternate, subrhombically ovate or elliptic-obovate, apex abruptly acute, base acute, 1–2 cm. wide × 2–3.5 cm. long, palmately 3- or faintly 5-nerved, bristly-ciliolate toward the apex, glandular-dotted, drying subcoriaceous, translucent; petioles 5–10 mm. long, clasping-decurrent; spikes terminal and axillary, 2 mm. thick × 3–5 cm. long, rather closely flowered; peduncle about 1 cm. long; bracts round-peltate; fruit globose, about 0.8 mm. long, apex oblique, stigma subapical.

Panama.

PANAMA: without location, *Hayes 811*. CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., June 28–July 2, 1938, *Woodson, Allen & Seibert 816, 895*.

This species very closely resembles *P. psiloclada* of Costa Rica.

45. PEPEROMIA PARIETARIAEFOLIA Trel. in Contr. U. S. Nat. Herb. 26:45. 1927.

A rather large, divaricately branched, glabrous herb; stem about 5 mm. thick below when dry, slender above, erect or ascending, up to 50 cm. or more tall, internodes 1 cm. long above to 5 cm. long below; leaves alternate, lance-elliptic, 1.2–2.5 cm. wide × 4–6 cm. long, apex acuminate, base acute, palmately rather conspicuously 5-nerved, the innermost pair of lateral nerves slightly confluent with the midrib near the base, ciliolate toward the apex, drying thin, subopaque, densely glandular-dotted beneath; petiole about 5 mm. long, clasping-decurrent; spikes axillary, 1 mm. thick × 5–6 cm. long, loosely to moderately flowered; peduncle 1 cm. long; bracts round-peltate; ovary ovoid, apex oblique, stigma subapical.

Southwestern Panama.

CHIRIQUÍ: Boquete District, Bajo Chorro, alt. 1800 m., *Davidson 346;* valley of Río Caldera, from El Boquete to the Cordillera, alt. 1400–1600 m., *Killip 3520.*

46. PEPEROMIA OBSCURIFOLIA C.DC. in Candollea 1:357. 1923.

Peperomia fatoana C.DC. loc. cit. 1923.
Peperomia obscurifolia var. *fatoana* Trel. in Contr. U. S. Nat. Herb. 26:47. 1927.
Peperomia obscurifolia var. *minor* Trel. loc. cit. 1927.
Peperomia Baileyae Trel. in Contr. Arn. Arb. 5:53. 1933.

A rather small, stoloniferous herb, growing on trees, logs, and rocks; stem 1–2 mm. thick, ascending to 10–15 cm., subappressed-villous, rooting at the nodes, internodes 1–3 cm. long below, reduced upward; leaves alternate, lance-elliptic or suboblanceolate, apex acute, base acute to cuneate, 1–1.5 cm. wide × 2–4 cm. long, or occasional leaves up to 2 × 5.5 cm., 5-nerved, the innermost pair of lateral nerves commonly coalescing with the midrib near the base, glabrous above or rarely

sparsely hairy along the nerves near the base, the nerves beneath usually sparsely hairy, ciliolate toward the apex, drying rather firm, subtranslucent, usually darker above, lighter beneath; petioles mostly 3–5 mm. long, channelled above, villous or with ciliate margins; spikes axillary and terminal, 1–1.5 mm. thick × 6–8 cm. long, rather closely flowered; peduncles 5–10 mm. long, soft-hairy; bracts round-peltate; fruit globose, about 0.5 mm. long, eventually on pseudopedicels, apex oblique, stigma subapical.

Central Panama.

COCLÉ: mountains beyond La Pintada, alt. 400–600 m., *Hunter & Allen 505;* El Valle de Antón and vicinity, alt. 500–700 m., *Seibert 453.* CANAL ZONE: Agua Clara, Trinidad River, alt. 10–40 m., *Pittier 3082, 3983;* between Matachin and Las Cascadas, *Cowell 330;* near Summit, Las Cascadas Plantation, *Standley 25726;* Barro Colorado Island, Gatún Lake, *Standley 31333; Bailey & Bailey 84.* COLÓN: Río Fató, alt. 10–1000 m., *Pittier 3902.*

There is considerable variation in the size of the leaves on the different specimens cited here but no more than is to be noted on certain individual specimens. There appear to be no other obvious characters by which the varieties recognized by Trelease can be maintained.

47. PEPEROMIA **Davidsonii** Yuncker, sp. nov.

Herba videtur statura moderata assurgens terrestris; caule superne dissite crispe-villoso, inferne glabrescente; foliis late ellipticis vel elliptico-obovatis, apice obtusis, basi abrupte acutis, palmatim 3-nerviis, utrinque dissite crispe-villosis, apicem versus ciliolatis; petiolo 5–15 mm. longo, crispe-villoso amplectenti-decurrente; spicis terminalibus axillaribusve; pedunculo 5–10 mm. longo, dissite crispe-villoso; ovario ovoideo, apice obliqua, stigmate subapicali.

A medium-sized, assurgent, terrestrial herb; stem 4 mm. thick when dry, ascending to 30 cm., sparsely crisp-villous above, glabrescent downward, internodes 1–2 cm. long; leaves alternate, broadly elliptic or elliptic-obovate, slightly constricted toward the obtuse apex, base abruptly acute, palmately 3-nerved, the midrib and lateral nerves with numerous slender, anastomosing branches, sparsely crisp-villous on both sides, at least along the nerves toward the base, 2–3.5 cm. wide × 3–6 cm. long, ciliolate toward the apex, drying membranous, translucent, fine glandular-dotted beneath; petioles 5–15 mm. long, grooved above, the groove crisp-villous, clasping-decurrent; spikes terminal and axillary, loosely flowered, 1 mm. thick × 3 cm. long; peduncle 5–10 mm. long, sparsely crisp-villous; bracts round-peltate; ovary ovoid, apex oblique, stigma subapical; fruit not matured.

Known only from the type locality.

CHIRIQUÍ: Volcán de Chiriquí, alt. 2850 m., July 18, 1938, *M. E. Davidson 1029* (U. S. Nat. Herb., TYPE).

The broadly elliptic or subobovate, obtuse, 3-nerved leaves, and crisp pubescence distinguish this species from *P. pascuicola* which it resembles to a considerable extent.

IV. KEY TO SPECIES WITH CYLINDRICAL OR ELLIPSOIDAL, BASALLY ATTACHED FRUIT, AND WITH APEX OBLIQUELY SCUTELLIFORM AND STIGMA MORE OR LESS CENTRAL, OR SLENDERLY ROSTRATE, AND STIGMA ANTERIOR NEAR THE BASE OF THE BEAK.

(Subgenus RYNCHOPHORUM (Miq.) Dahlst. in part).

a. Fruit mostly more or less cylindrical, sometimes thicker downward, apex obliquely scutelliform.
  b. Leaves subpeltate..... 61. P. CORDULATA
  bb. Leaves not at all peltate.
    c. Plants conspicuously black-dotted..... 38. P. GLABELLA
    cc. Plants not black-dotted, glands, if present, not black.
      d. Petioles mostly less than 5 mm. long, stout.
        e. Stems and leaves glabrous..... 48. P. PORTOBELLENSIS
        ee. Stems and/or petioles villous when young and/or about the nodes, leaves mostly drying more or less coriaceous and opaque.. 49. P. CAUDULILIMBA
      dd. Petioles mostly 5–20 mm. long, not markedly stout, leaves mostly drying membranous and translucent.
        e. Petioles and/or young stems, if hairy, minutely hirtellous..... 50. P. OBLONGIBACCA
        ee. Petioles somewhat villous-ciliate, stems glabrous or the nodes sparsely villous..... 50c. P. OBLONGIBACCA var. SUBVILLOSA

aa. Fruit mostly ellipsoidal, apex more or less slenderly rostrate, stigma anterior.
  b. Leaves palmately nerved, or essentially so.
    c. Leaves mostly 1–2 cm. long, as wide as long, apex scarcely protracted..... 51. P. SERPENS
    cc. Leaves mostly larger.
      d. Spikes on axillary stalks..... 52. P. UROCARPOIDES
      dd. Spikes on leaf-opposed stalks.
        e. Leaves narrowly peltate, strongly red-glandular..... 65. P. PERGLANDULOSA
        ee. Leaves not peltate nor strongly red-glandular..... 53. P. DIGITINERVIA
  bb. Leaves pli- or pinnately-nerved.
    c. Leaves elliptic-ovate, base rounded..... 54. P. DISTACHYA
    cc. Leaves not ovate, base mostly acute to cuneate.
      d. Leaves puberulent above, scarcely more than 5 cm. long..... 55. P. MACHAERODONTA
      dd. Leaves glabrous, or obscurely hirtellous along the midrib beneath, mostly larger.
        e. Peduncle minutely hirtellous.
          f. Bracts strongly imbricated..... 56b. P. OBTUSIFOLIA var. LONGIBRACTEATA
          ff. Bracts scarcely imbricated, mostly 0.3–0.4 mm. wide; fruit beak slender, terete, strongly hooked..... 56. P. OBTUSIFOLIA
        ee. Peduncle glabrous, bracts mostly 0.5 mm. wide; fruit beak gradually narrowed from a wide base, not strongly hooked..... 57. P. MAGNOLIAEFOLIA

48. PEPEROMIA PORTOBELLENSIS Beurl. Sv. Vet.-Akad. Handl. 1854:147. 1856.

A glabrous, subsimple herb, rooting from the nodes; leaves alternate, oblong, apex acuminate, base obtusish, 1–2.5 cm. wide × 5–7.5 cm. long, obscurely 5-nerved; petiole very short; spikes opposite the leaves, pendent, subulate-filiform, 10 cm. long; fruit oblong, granular, apex obliquely scutelliform, stigma central on the scutellum.

Porto Bello, Colón.

COLÓN: Porto Bello, *Bilberg*.

This species, the type of which has not been examined, appears to be very closely related to *P. caudulilimba*. As described, it appears to differ in its glabrous plants and 5-nerved leaves. However, some leaves of *P. caudulilimba* may be 5-

nerved with an obscure outer pair of lateral nerves, and the stems and leaves are sometimes nearly glabrous. It is possible that further study may show that this and *P. caudulilimba* are different forms of the same species.

49. Peperomia caudulilimba C.DC. in Ann. Conserv. & Jard. Bot. Genève 21:269. 1920.

Peperomia gatunensis C.DC. in Candollea 1:363. 1923.
Peperomia piperorum Trel. in Contr. U. S. Nat. Herb. 26:49. 1927.
Peperomia caudulilimba var. *cryptopoda* Trel. loc. cit. 1927.
?*Peperomia caudulilimba* var. *longependula* C.DC. loc. cit. 1920.

A moderate-sized, often long-pendent, arboricolous herb; stem 2–3 mm. thick when dry, rooting from the lower nodes, branches often long and pendent, more or less villous, usually at least about the nodes, internodes up to 7–8 cm. long below, reduced upward; leaves alternate, lanceolate or lance-elliptic, apex narrowly sharp-acuminate, base somewhat rounded, obtuse or subacute, mostly 1–2.5 cm. wide × 4–8 cm. long, occasionally up to 4 × 11 cm., glabrous on both sides, or rarely sparsely hairy beneath, pinnately nerved from below the middle with two pair of nerves approximated near the base and a third pair toward the middle, usually more or less ciliate, mostly somewhat yellow glandular-dotted beneath, drying coriaceous, opaque; petiole less than 5 mm. long, stout, commonly ciliate; spikes solitary or often paired on bracted stalks 5–10 mm. long, closely flowered, 1–2 mm. thick × 8–12 cm. long; peduncle glabrous or sparsely hairy, 1–1.5 cm. long; bracts round-peltate; fruit reddish, cylindrical, about 2 mm. long, apex obliquely truncate, scutelliform, stigma central on the scutellum.

Panama.

Bocas del Toro: Old Bank Island, vicinity of Chiriquí Lagoon, *von Wedel 1872*; Water Valley, *von Wedel 1690*; Farm 6, Changuinola Valley, *Dunlap 486*. Coclé: above Penonomé, *Williams 366*. Canal Zone: *Cowell 23919*; railroad relocation between Gorgona and Gatún, alt. 10–50 m., *Pittier 2280*; Río Agua Salud, near Frijoles, *Piper 6035*; vicinity of Fort Sherman, *Standley 31118*; forest along the Río Indio de Gatún, near sea-level, *Pittier 2788*; *Maxon 4818, 4864*; near Río Medio, *Miller 1735* near Salamanca Hydrographic Station on the gorge of the Río Pequení, alt. 70–80 m., *Dodge, Steyermark & Allen 16082*; Barro Colorado Island, Gatún Lake, *Standley 31321, 31356, 41167*. Darién: Boca de Panarandó, on Sambú River, alt. 20 m., *Pittier 5571*.

49a. Peperomia caudulilimba var. **cylindribacca** (C.DC.) Yuncker, comb. nov.

Peperomia cylindribacca C.DC. in Candollea 1:370. 1923.

Leaves 4–5 cm. wide × 9–11 cm. long, densely ciliate; fruit 2.5 mm. long, scutellum acute.

Known only from the type locality.

Chiriquí: vicinity of San Felix, alt. 0–120 m., Dec. 1911, *Pittier 5273* (U. S. Nat. Herb., type).

This species is one of a series, including *P. macrostachya* of South America, which appears to be very closely related and may, indeed, represent only variations of a single polymorphic species. Careful field observations, including mass collec-

tions, are needed to interpret adequately the various forms which have been described. It is very closely related to *P. oblongibacca* from which it differs because of its mostly shorter petioles, more coriaceous leaves, and with villous rather than hirtellous type of pubescence.

50. PEPEROMIA OBLONGIBACCA C.DC. in Candollea 1:288. 1923.

A moderate-sized, epiphytic herb; stem 2–3 mm. thick, branches somewhat pendulous, glabrous or obscurely and minutely hirtellous, internodes mostly 2–3 cm. long; leaves alternate, elliptic, lance-elliptic or suboblanceolate, apex sharply long-acuminate, base acute to cuneate, glabrous on both sides, loosely ciliate, 5- or obscurely 7-plinerved from below the middle, glandular-dotted beneath, drying thin, translucent; petiole slender, up to 2 cm. long below, reduced upward; spikes 1, 2, or sometimes 3 on short, bracted, sympodial branches, 1–1.5 mm. thick × 15–20 cm. or more long, closely flowered, peduncle 1 cm. long, obscurely hirtellous glabrescent; bracts comparatively large, round-peltate; fruit subcylindrical, 2–3 mm. long, apex obliquely scutelliform, stigma central on the scutellum.

Río Fató, Colón.

COLÓN: along Río Fató, in forests or thickets, alt. 10–100 m., *Pittier 3891*.

KEY TO THE VARIETIES OF P. OBLONGIBACCA

a. Minutely puberulent on young growth, or glabrous; petioles not ciliate.
  b. Leaves 6–7 cm. long.
    c. Leaf base subcuneate; stems obscurely hirtellous ..... P. OBLONGIBACCA
    cc. Leaf base acute; stems puberulent ..... var. MARRAGANTINA
  bb. Leaves 10–12 cm. long ..... var. MACROPHYLLA
aa. Nodes more or less sparsely villous; petioles ciliate ..... var. SUBVILLOSA

Fig. 19. *Peperomia oblongifolia* var. *macrophylla*

50a. PEPEROMIA OBLONGIBACCA var. **marragantina** (C.DC.) Yuncker, comb. nov.

Peperomia caudulilimba var. *marragantina* C.DC. in Candollea 1:382. 1923, as *marregantina*, name only.

Young growth velvety-puberulent; leaves lance-ovate.

Known only from the type locality.

PANAMÁ: Marragantí, April 6, 1903, *Williams 694* (U. S. Nat. Herb., TYPE).

50b. PEPEROMIA OBLONGIBACCA var. **macrophylla** Yuncker, var. nov.

Caule juvenili minute hirtello vel glabrato; foliis 7-plinerviis.

Young growth obscurely and minutely hirtellous or glabrous; leaves 3.5–5 cm. wide × 12–14 cm. long, 7-plinerved.

Known only from the type locality.

CANAL ZONE: drowned forest near Vigia and San Juan on Río Pequení, alt. 66 m., Nov. 26, 1934, *Dodge, Steyermark & Allen 16522* (Herb. Missouri Bot. Gard., TYPE).

50c. PEPEROMIA OBLONGIBACCA var. **subvillosa** Yuncker, var. nov.

Caulibus ad nodos dissite villosis; foliis ovatis, 5–7-plinerviis; petiolo ciliato.

Nodes more or less sparsely villous; leaves ovate, 5- to 7-plinerved; petiole commonly ciliate.

Known only from the type locality.

CANAL ZONE: near Río Medio, Feb. 11, 1937, *Miller 1740* (U. S. Nat. Herb., TYPE).

The plants included here are all obviously rather closely related but differ in the characters as described. It is not believed that they represent individual species and there may be some question regarding their status even as varieties.

51. PEPEROMIA SERPENS (Sw.) Loud. Hort. Brit. 13. 1830.

Piper serpens Sw. Prodr. Veg. Ind. Occ. 16. 1788.
Peperomia scandens Ruiz & Pav. Fl. Peruv. & Chil. 1:32, *pl. 51, 5.b.* 1798.
Piper scandens Vahl, Enum. 1:346. 1804, not Sw. 1788.
Piper bracteatum Thomps. in Trans. Linn. Soc. 9:203, *pl. 21.* 1808.
Peperomia repens H.B.K. Nov. Gen. & Sp. 1:65. 1815.
Peperomia reniformis Hook. Exot. Fl. 3:*pl. 164.* 1827.
Piper Guildingianum Spreng. Syst. Veg. 4. Cur. Post. 21. 1827.
Peperomia pulicaris Opiz in Presl, Reliq. Haenk. 1:162, *pl. 30.* 1830.
Peperomia myosurus hb. Willd. in A. Dietr. Sp. Pl. 1:159. 1831.
Peperomia Guildingiana A. Dietr. loc. cit. 162. 1831.
Piper myosurus hb. Willd. in D. Dietr. Syn. Pl. 1:110. 1839.
Verhuellia serpens Miq. Syst. Pip. 49. 1843.
Acrocarpidium pulicare Miq. loc. cit. 57 1843.
Acrocarpidium repens Miq. loc. cit. 59. 1843.
Acrocarpidium scandens Miq. loc. cit. 1843.
Piper herbaceum Miq. loc. cit. 1843.
Acrocarpidium Guildingianum Miq. in Hook. Lond. Jour. Bot. 4:412. 1845.
?*Peperomia reptans* C.DC. in Jour. Bot. 4:143. 1866.
?*Peperomia scandens* var. *fertilior* C.DC. in DC. Prodr. 16[1]:434. 1869.

A comparatively small, creeping or scandent herb; stem slender, crisp-pubescent; leaves alternate, round-subdeltoid, mostly 1–2 cm. wide or occasionally up to 3 cm., apex acute or obtuse, base truncate-cordulate, palmately 3- to 5-nerved, drying rather membranous and thin, more or less crisp-pubescent on both sides; petiole 5–30 mm. long, crisp-pubescent; spikes axillary and sympodially terminal, up to 3 cm. long; peduncle 1- or rarely 2-bracted, usually about as long as the spike, crisp-pubescent; floral bracts round-peltate; fruit about 1 mm. long, ellipsoidal, stigma at the base of the slender, pointed beak.

West Indies, and on the mainland southward from Panama to Brazil and Peru.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1034.* CANAL ZONE: Río Indio de Gatún, near sea-level, *Maxon 4857.*

52. PEPEROMIA UROCARPOIDES C.DC. in Candollea 1:362. 1923.

A rather small, repent, crisp-hairy herb; stem 1–2 mm. thick, rooting from the nodes, internodes mostly 2–3 cm. long; leaves alternate, ovate, apex gradually bluntly pointed, base rounded, obtuse, cordulate, or acutish at the petiole, 1.5–3

cm. wide × 2–3.5 cm. long, crisp-pubescent on both sides, ciliate, palmately 5-nerved, the nerves branched upward, more or less glandular-dotted, drying subcoriaceous, subopaque; petiole 1–2 cm. long, crisp-pubescent; spikes axillary or terminal, 1 mm. thick × 3 cm. long; peduncle crisp-pubescent, 1 cm. or more long, bracteate at about the middle; floral bracts round-peltate; fruit oblong, obliquely slender-mucronate, stigma near the base of the beak.

Panama.

COCLÉ: mountains beyond La Pintada, alt. 400–600 m., *Hunter & Allen 571*. DARIÉN: Cerro de Garagará, Sambú basin, southern Darién, alt. 500–974 m., *Pittier 5670*.

This species differs from *P. urocarpa* in the shape of the 5-nerved leaves, etc.

53. PEPEROMIA DIGITINERVIA Trel. in Ann. Mo. Bot. Gard. 27:302. 1940.

A repent, epiphytic herb; stem 1–2 mm. thick, rooting at the nodes, rather densely crisp-puberulent, internodes 2–4 cm. or more long; leaves alternate, ovate, apex acute, base subtruncate, cordulate or acute at the petiole, 2–3 cm. wide × 2.5–4 cm. long, subpalmately 5-nerved, the innermost pair of lateral nerves coalescing with the midrib within the lowermost 2–3 mm., sparsely pubescent above, paler and crisp-puberulent beneath, at least along the nerves, ciliate, drying coriaceous, subopaque; petiole 1–3.5 cm. long, pubescent glabrescent, channelled above; spikes leaf-opposed, 2 mm. thick × 3.5 cm. long, densely flowered; peduncle 2 cm. long, crisp-puberulent, 1-bracteate near the middle; floral bracts round-peltate; fruit ellipsoidal, about 0.8 mm. long, rostrate, stigma anterior at the base of the beak.

El Valle, Coclé.

COCLÉ: vicinity of El Valle, alt. 600–1000 m., *Allen 1221*.

This species resembles *P. cubensis* to some extent but differs because of the pubescence, smaller leaves, etc.

54. PEPEROMIA DISTACHYA (L.) A. Dietr. Sp. Pl. 1:156. 1831.

Piper distachyon L. Sp. Pl. 1:30. 1753.
Peperomia producta Griseb. Fl. Br. W. Ind. 166. 1864.
Peperomia Bakerii C.DC. in Urb. Symb. Ant. 5:296. 1907.

A sparsely hairy or glabrate, creeping or sometimes scandent herb; stems 2–3 mm. thick, rooting at the nodes; leaves alternate, elliptic-ovate, 4–5 cm. wide × 7–8.5 cm. long, apex acuminate, typically rounded at the base and sometimes cordulate or barely subpeltate, drying rather thin and dull, sparsely hairy beneath when young, or glabrous on both sides, ciliolate towards the apex, 9-plinerved with the nerves coalescing below the middle; petiole 3–5 or sometimes even 9 cm. long, glabrous or somewhat ciliate; spikes 3–5 cm. or more long, mostly paired at the ends of terminal or axillary stalks 3–4 cm. long; peduncle scarcely 2 cm. long; bracts round-peltate; fruit ellipsoidal, rostrate, stigma at the base of the beak.

Common in the West Indies. Apparently rare in Panama. Also reported from the Guianas and Ecuador.

BOCAS DEL TORO: Fish Creek, vicinity of Chiriquí Lagoon, *von Wedel 2193*. COCLÉ: mountains beyond La Pintada, alt. 400–600 m., *Hunter & Allen 573*. PANAMÁ: summit of Cerro Campaña, alt. 800–1000 m., *Allen 2224*.

55. PEPEROMIA MACHAERODONTA Trel. in Contr. U. S. Nat. Herb. 26:47. 1927.

A rather small, suberect, epiphytic herb; stem 3 mm. thick, simple, ascending to 10 cm. or more, glabrous, drying wrinkled, yellow-glossy, internodes 1–2 cm. long; leaves alternate, elliptic, round-elliptic, or subobovate, apex abruptly short-acuminate, base acute or subrounded, glabrescent beneath, crisp-puberulent above, especially along the nerves, pinnately nerved to above the middle, the nerves about 4 on each side, 2–3 cm. wide × 3–5.5 cm. long, drying coriaceous, opaque, somewhat glossy-wrinkled, especially near the margin, with scattered glandular-dots; petiole 5–10 mm. long, glabrous, yellow-glossy, channelled above; spikes terminal, 2 mm. thick × 6–8 cm. long, rather closely flowered; peduncle 1.5–2.5 cm. long, glabrous; bracts round-peltate, pale-glandular-dotted; fruit ellipsoidal, about 1 mm. long, rostrate, stigma anterior near the base of the pale, subterete, erect, slightly curved, equilong beak.

Valley of the Río Piarnasta, east of El Boquete, Chiriquí.

CHIRIQUÍ: valley of Río Piarnasta, about 5 miles east of El Boquete, alt. 1525–1600 m., *Killip 3538*.

The rather small plants, puberulent upper leaf surface, small, pinnately nerved leaves, and type of fruit characterize this species.

56. PEPEROMIA OBTUSIFOLIA (L.) A. Dietr. Sp. Pl. 1:154. 1831.

Piper obtusifolium L. Sp. Pl. 30. 1753.
?Piper cuneifolium Jacq. Collect. 4:127, *pl. 214*. 1788.
Piper humile Mill. Gard. Dict. no. 4, ex Poir. in Lam. Encycl. Meth. 5:473. 1804, fide C.DC. in Urb. Symb. Ant. 3:254. 1902
Piper Milleri Roem. & Schult. Syst. Veg. 1:337. 1817, fide C.DC. loc. cit. 1902.
Peperomia hemionitidifolia Ham. Prodr. Pl. Ind. Occ. 2. 1825, fide C.DC. in Urb. Symb. Ant. 3:254. 1902.
?Peperomia cuneifolia A. Dietr. Sp. Pl. 1:146. 1831.
Peperomia commutata Trel. in Fedde Rep. Sp. Nov. 23:29. 1926, in part.
Peperomia bayatana Trel. loc. cit. 30. 1926.
Peperomia daiquiriana Trel. loc. cit. 1926.
Peperomia Lunana Trel. loc. cit. 1926.
Peperomia Earlei Trel. loc. cit. 31. 1926.
Peperomia dodecatheontophylla Trel. in Contr. U. S. Nat. Herb. 26:48. 1927.
Peperomia Antoni var. *reducta* Trel. in Ann. Mo. Bot. Gard. 27:299. 1940.

A fleshy, stoloniferous-assurgent, terrestrial or epiphytic herb, glabrous except for the peduncle which is minutely hirtellous as is also sometimes the lower leaf-surface; stem up to 5 mm. thick when dry, ascending to 15 cm. or more from the prostrate, rooting base, internodes mostly 2–3 cm. long; leaves alternate, elliptic-obovate, 3–8 cm. wide × 5–20 cm. long, occasional specimens with smaller leaves, but commonly about 4–6 × 8–12 cm., apex rounded, obtuse, sometimes slightly emarginate, base cuneate, 7- to 11-plinerved from below the middle, the midrib branched upward, drying more or less coriaceous, opaque; petiole mostly 1.5–4

cm. long, or occasionally somewhat longer, more or less winged by the decurrent blade; spikes 2–4 mm thick × 5–15 cm. long, densely flowered, solitary or paired on a 1-bracted, terminal, leaf-opposed, or occasionally axillary, usually minutely hirtellous stalk 3–5 cm. or more long; floral bracts 0.3–0.4 mm. wide, round-peltate; fruit ellipsoidal, about 1.25 mm. long including the slender, erect, terminally hooked beak, stigma anterior at the base of the beak.

General in the West Indies and on the mainland from Mexico through Central America and northern South America.

COCLÉ: vicinity of El Valle, alt. 600–1000 m., *Allen 1222.* CANAL ZONE: along Río Indio de Gatún, *Pittier 2800;* Summit, *Lindsay 402.*

56a. PEPEROMIA OBTUSIFOLIA var. EMARGINATA (Ruiz & Pav.) Dahlst. in Kgl. Sv. Vet.-Akad. Handl. 33^2:66. 1900.

Peperomia emarginata Ruiz & Pav. Fl. Peruv. & Chil. 1:33, *pl. 49, f.a.* 1798.
Piper emarginatum Vahl, Enum. Pl. 1:339. 1804.

Stems short; leaves oblong-elliptic-obovate, apex somewhat narrowed and rounded, emarginate, mostly 2 to 3 times longer than wide; spikes 2–3 mm. thick, up to 8–15 cm. long, single, or more commonly divergently paired on a common, terminal, or leaf-opposed stalk 1–4 cm. long, or occasionally subpaniculately 3-spiked; fruit about 1 mm. long.

Found with the species.

VERAGUAS: vicinity of Santa Fé, forested slopes of Cerro Tute, alt. 900 m., *Allen 4334.* CANAL ZONE: near Salamanca Hydrographic Station on the gorge of the Río Pequení, 70–80 m., *Dodge, Steyermark & Allen 16525, 16525b;* near Río Medio, *Miller 1736.*

Fig. 20. *Peperomia obtusifolia* var. *longibracteata*

56b. PEPEROMIA OBTUSIFOLIA var. **longibracteata** Yuncker, var. nov.

Foliis ellipticis; spicis 3 in panicula elongata laxa axillari bracteata dispositis, bracteis lineari-lanceolatis usque ad 3 cm. longis; pedunculo 2–4 cm. longo minute hirtello; ovario ellipsoideo rostrato.

Leaves elliptic, 4–5 cm. wide × 10–12 cm. long; spikes 3 mm. thick × 5 cm. or more long, in a 3-spicate, elongate, loosely paniculate, axillary inflorescence, the main stalk 8–10 cm. long, individual peduncles 2–4 cm. long, minutely hirtellous, in the axils of linear-lanceolate bracts up to 3 cm. long; floral bracts subquadrangular-peltate, strongly imbricate in young spikes; ovary ellipsoidal, rostrate, stigma at the base of the beak; fruit not matured.

South-central Panama.

COCLÉ: region north of El Valle de Antón, alt. 1000 m., Sept. 27, 1946, *Allen 3730* (Herb. Missouri Bot. Gard., TYPE); La Mesa, Aug. 31, 1941, *Allen 2728.*

This species exhibits great variation in the size and shape of the leaves and length of the spikes, sometimes on the same plant. It has not been possible to maintain as distinct the several species proposed by Trelease. The variability of the plants, readily observed in the field, leads one to conclude that only one species is represented. The hirtellous peduncle and commonly also the lower leaf surface, much smaller bracts, and more slender and strongly hooked beak of the fruit distinguish it from *P. magnoliaefolia.*

Variety *longibracteata* bears considerable resemblance to many specimens believed unquestionably to represent *P. obtusifolia.* The elongated 3-spicate, long-bracteate, paniculate inflorescence, and strongly imbricated floral bracts are rather strong differential characters. Additional collections may show that this variety merits specific status. In the meantime, however, it is given a rather questionable varietal status. The axillary inflorescence, etc. distinguishes it from *P. magnoliaefolia,* and the leaf shape and size, especially, from *P. Williamsii.*

57. Peperomia magnoliaefolia (Jacq.) A. Dietr. Sp. Pl. 1:153. 1831.

Piper magnoliaefolium Jacq. Collect. 3:210. 1789.
Piper subrotundum Haw. Rev. Pl. Succ. 2. 1819.
Peperomia subrotunda A. Dietr. loc. cit. 154. 1831.
Peperomia amplexicaulis (Sw.) A. Dietr. var. *magnoliaefolia* (A. Dietr.) Griseb. Fl. Br. W. Ind. 176. 1859.
Peperomia euosma Trel. in Fedde Rep. Sp. Nov. 23:29. 1926.
Peperomia Antoni Trel. in Ann. Mo. Bot. Gard. 24:185. 1937.
Peperomia Antoni f. *fertilior* Trel. loc. cit. 27:299. 1940.
Peperomia Antoni f. *lutea* Trel. loc. cit. 300. 1940.

A moderately large, assurgent, glabrous, succulent herb; stem 3–5 mm. thick, rooting at the lower nodes, ascending to 25 cm. or more, internodes mostly 1–5 or 6 cm. long; leaves alternate, round, obovate-elliptic, or subspatulate, 3–8 cm. wide × 6–15 cm. long, apex rounded, often emarginate, base cuneate or sometimes rather abruptly contracted, drying dull, coriaceous, opaque, 7- to 9-plinerved from near the base, the rather prominent midrib pinnately branched upward, the lateral nerves slender and obscure; petiole 1–3 cm. long, more or less winged by the decurrent blade; spikes 3 mm. thick and up to 15–18 cm. long, closely flowered, 1–2 or sometimes 3 on a terminal or leaf-opposed, bracted stalk 5–10 cm. long; peduncle 1.5–3 cm. long, glabrous or rarely obscurely hirtellous; floral bracts round-peltate, mostly about 0.5 mm. wide; fruit about 1.25 mm. long, ellipsoidal, rostrate, the beak gradually narrowed from a broad base, from one-fourth to as long as the fruit, sharp and more or less curved but usually not hooked at the apex; stigma at the base of the beak.

West Indies, Panama, and northern South America.

Bocas del Toro: Careening Cay, Isla Colón, alt. 0–120 m., *von Wedel 565.* Coclé: El Valle de Antón and vicinity, alt. 500–700 m., *Seibert 437;* alt. 800–1000 m., *Allen 760, 1160,* collection labelled "lata" on the herbarium sheets; between Las Margaritas and El Valle, *Woodson, Allen & Seibert 1208.* Canal Zone: Experimental Gardens, *Stanwood 402.*

This species is closely related to *P. obtusifolia* from which it is to be distinguished, however, because of its glabrous peduncles and lower leaf surface, wider floral bracts, and with the fruit beak mostly stouter and ordinarily not hooked at the end.

58. PEPEROMIA HISPIDULA (Sw.) A. Dietr. Sp. Pl. 1:165. 1831.

Piper hispidulum Sw. Prodr. Veg. Ind. Occ. 15. 1788.
Acrocarpidium hispidulum Miq. Syst. Pip. 54. 1843.
Acrocarpidium Sellovianum Miq. loc. cit. 55. 1843.
?Peperomia tenera Miq. in Mart. Fl. Brasil. 4^1:19, *pl. 1, f. 1.* 1852.
?Peperomia pilinervia C.DC. in Bull. Herb. Boiss. 6:509. 1898.
?Peperomia hispidula var. *Sellowiana* Dahlst. in Kgl. Sv. Vet.-Akad. Handl. 33^2:14. 1900.
Peperomia perhispidula C.DC. in Engl. Bot. Jahrb. 40:257. 1908.
Peperomia hispidula var. *perhispidula* C.DC. in Candollea 1:335. 1923.
Peperomia Woodsonii Trel. in Ann. Mo. Bot. Gard. 27:305. 1940.

A rather small, assurgent, branched, spreading herb; stem 2–3 mm. thick below when dry, branches ascending to 20 cm. or more from the decumbent, rooting base, hispid at least at the nodes, the hairs rigid to rather flaccid, internodes variable in length; leaves alternate, ovate-orbicular or rhombic-ovate, 8–15 mm. in diameter, apex rounded, obtuse, base rounded or triangular, obtuse, loosely hispid above or glabrate, loosely hispid beneath at least along the nerves, palmately 5-nerved with the midrib strongly branched at about the middle, drying membranous and subpellucid; petiole commonly 5–15 mm. long, slender, hispid to glabrate, but usually with at least a few hairs near the blade; spikes leaf-opposed or terminal, slender, mostly 1–2 cm. long, loosely and alternately flowered; peduncle slender, 10–15 mm. long, hispid to glabrate; bracts round-peltate; fruit globose-ovoid, about 1 mm. long, covered with white, hispid hairs and on a pedicel up to 0.5 mm. long when mature, stigma apical on a conic style.

West Indies, Central America, and northern South America. Apparently infrequent in Panama.

CHIRIQUÍ: vicinity of Casita Alta, Volcán de Chiriquí, alt. 1500–2000 m., *Woodson, Allen & Seibert 933.*

Dahlstedt included this species in the subgenus ACROCARPIDIUM (Miq.) Hensch.

VI. KEY TO SPECIES WITH PELTATE LEAVES

a. Fruit scarcely rostrate, apex acute, mammiform, or obliquely scutelliform.
  b. Stems very short, scarcely 1 cm. long; rachis strongly hispidulous..... 59. P. HISPIDORHACHIS
  bb. Stems much longer.
    c. Leaves pubescent beneath; petioles more than half as long as the blade, slender..... 60. P. CERRO-PUNTANA
    cc. Leaves glabrous; petioles shorter, stout..... 61. P. CORDULATA
aa. Fruit rostrate.
  b. Petiole attached 1–2 cm. or more from the leaf margin.
    c. Main lateral nerves conspicuous and strongly curved toward the apex..... 62. P. FLEXINERVIA
  cc. Main lateral nerves rather obscure and ascending more sharply.
    d. Leaves mostly 6–8 cm. wide..... 63. P. CILIIFERA
    dd. Leaves mostly 5 cm. or less wide..... 64. P. CONSERTA

bb. Petiole attached within 1 cm. of the margin.
c. Leaves 10 cm. or more long ..... 65. P. MACULOSA
cc. Leaves 3 cm. or less long ..... 66. P. PERGLANDULOSA

59. PEPEROMIA **hispidorhachis** Yuncker, sp. nov.

Herba parva epiphytica; caule perbreve; foliis alternis ovato-lanceolatis, apice sensim acutis, basi rotundatis ca. 5 mm. et basi peltatis utrinque dissite crispe-villosis (pilis usque ad 1 mm. longis), ciliatis, palmatim 7–9-nerviis luteo-glanduloso-punctatis; petiolo gracili 4–5 mm. longo dissite villoso, ad basim dilatato; spicis axillaribus; pedunculo filiformi spicam ipsam aequante, rhachi conferte hispido; drupa angusto-ellipsoidea, breve-pedicellata, apice subobliquo, stigmate apicali.

Fig. 21. *Peperomia hispidorhachis*

A small, epiphytic plant; stem very short, scarcely 1 cm. long × 3 mm. thick, tumid with thickened leaf scars; leaves alternate, ovate-lanceolate, apex gradually acute, base rounded, peltate about 5 mm. above the base, 2.5–4 cm. wide × 6–8.5 cm. long, loosely crisp-villous on both sides, the hairs up to 1 mm. long, ciliate, palmately 7- or in large leaves faintly 9-nerved, the innermost pair of lateral nerves coalescing with the midrib within the lowermost 5-10 mm., the lateral nerves simple or in large leaves more or less forked, drying very thin, pellucid, yellow-glandular-dotted; petiole slender, 4–5 cm. or more long, loosely villous, base much enlarged; spikes axillary, scarcely 1 mm. thick, 7–9 cm. or more (?) long, loosely flowered; peduncle filiform, about as long as the spike, loosely villous; rachis densely and prominently hispid; bracts round-peltate; fruit narrowly ellipsoidal, apex slightly oblique, narrowed toward the base to form a short stalk, stigma essentially apical.

Known only from the type locality.

PANAMÁ: Río La Maestra, alt. 0–25 m., Dec. 4, 1936, *Allen 31* (Herb. Missouri Bot. Gard., TYPE).

This species bears some resemblance to *P. tecticola* of Costa Rica. It differs, however, according to DeCandolle's description, because of the leaf shape, shorter spikes, hispid rachis, and shape of the substalked fruit. It closely resembles *P. Killipi* in general appearance. It differs, however, because of its villous, definitely peltate leaves, strongly hispid rachis, and fruit shape.

60. PEPEROMIA CERRO-PUNTANA Trel. in Ann. Mo. Bot. Gard. 27:301. 1940.

A terrestrial or epiphytic mountain herb; stem 2–3 mm. thick, more or less decumbent and rooting from the lower nodes, glabrous, internodes 2–5 or 6 cm. long; leaves alternate, round-ovate or ovate, apex slender-acuminate, base round, obtuse, peltate about 1 cm. from the margin, 4–5 cm. wide × 6–8 cm. long, glabrous above, loosely pubescent beneath, the hairs about 0.5 mm. long, drying rather membranous, translucent; petiole slender, up to 7 cm. long, clasping, sparsely hairy glabrescent; spikes leaf-opposed, 2–3 mm. thick × 7–12 cm. long, moderately flowered; peduncle 2–3 mm. long, pubescent; rachis somewhat papillate; bracts

round-peltate; ovary obovoid-turbinate, stigma apical.

Mountains of Chiriquí province.

CHIRIQUÍ: trail from Cerro Punta to headwaters of Río Caldera, alt. 2250–2500 m., *Allen 1451;* Bajo Chorro, Boquete District, in rain forest, alt. 1800 m., *Davidson 219.*

The peltate leaves with villous lower surface, rather long spikes, and subturbinate ovary with apical stigma are distinctive characters of this species.

61. PEPEROMIA CORDULATA C.DC. in Jour. Bot. 4:137. 1866.

A pendent, glabrous, epiphytic herb; stem 5 mm. thick when dry, internodes 2–4 or 6 cm. long; leaves alternate, round-ovate or ovate, apex acute to subacuminate, base rounded, peltate within 1 cm. of the margin, 5–8 cm. wide × 7–11 cm. long, palmately about 11-nerved, drying rather firm, subtranslucent; petioles stout, 2–3 mm. thick, 1–4 cm. long; spikes on short, bracteate, leaf-opposed branches, 2 mm. thick × 15 cm. long, densely flowered; peduncle 1.5–2 cm. long, bracts rather large, lanceolate; floral bracts round-peltate; fruit subglobose, apex obliquely truncately scutelliform, stigma central.

Panama.

CANAL ZONE: near Madden Dam and along Azote Caballo Road near Alahuela, alt. 90–100 m., *Dodge 16595.* COLÓN: Chagres, *Fendler 265.*

62. PEPEROMIA **flexinervia** Yuncker, sp. nov.

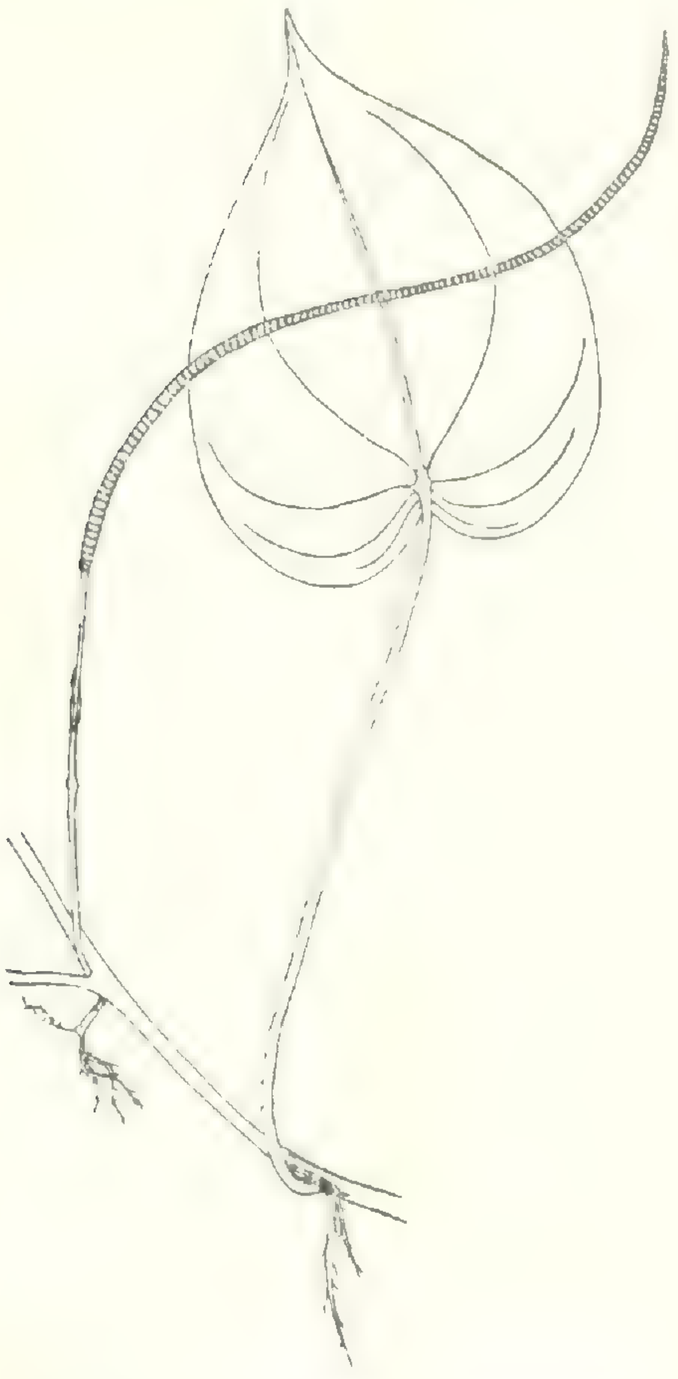

Fig. 22. *Peperomia flexinervia*

Herba repens terrestris carnosula fere tota glabra; foliis alternis, rotundato-ovatis, apice sensim acute acuminatis, e basi rotundatis vel cordatis, peltatis ad 15 mm. procul ex margine, ex petiolo 7–9-nerviis, conferte ciliatis, glanduloso-punctatis; petiolo usque ad 16 cm. longo; spicis axillaribus, usque ad 20 cm. longis, singulis e caudiculo 1–2-bracteato; ovario ovoideo, rostrato.

A repent, succulent, terrestrial, essentially glabrous herb; stem creeping, 3 mm. thick when dry, rooting at the nodes, "densely pink-spotted," internodes 6–10 cm. or more long; leaves alternate, round-ovate, apex attenuately sharp-acuminate, base rounded to cordate, peltate within 15 mm. of the margin, rather prominently 7- to 9-nerved from the petiole, the lateral nerves strongly curving toward the apex, the innermost pair slightly coalescent with the midrib which is faintly branched upward, 7–9 cm. wide × 12–15 cm. long, glabrous, yellow-glandular-dotted, densely ciliate, drying firm, subopaque, finely pellucid-dotted; petiole up to 16 cm. or more

long; spikes axillary, up to 20 cm. or more long, solitary or sometimes multiple (?), on a 1- or 2-bracted stalk up to 10 cm. or more long, bracts 2 cm. or more long, narrowly lanceolate; floral bracts round-peltate; ovary ovoid, rostrate, stigma at the base of the beak; fruit not developed.

Known only from the type locality.

COCLÉ: Las Minas, Sept. 1, 1941, *Allen 2738* (Herb. Missouri Bot. Gard., TYPE).

This species resembles *P. parmata* of Costa Rica but differs in the creeping habit of growth, and type of venation. From *P. maculata* it differs especially in the shape of the leaves and type of venation.

63. PEPEROMIA CILIIFERA Trel. in Contr. U. S. Nat. Herb. 26:212. 1929.

Peperomia hernandifolia (Vahl) A. Dietr. var. *ciliifera* Trel. in Bot. Gaz. 73:145. 1922.

A repent, glabrous, vine-like herb; stem 3–4 mm. thick when dry, rooting at the nodes, internodes up to 12 cm. or more long; leaves alternate, round-ovate, apex abruptly sharp-acuminate, base round, obtuse, peltate 2–3 cm. from the margin, rather densely ciliate, at least when young, 6–10 cm. wide × 9–15 cm. long, obscurely about 9-nerved from the petiole, drying dark, coriaceous, opaque; petioles up to 12 cm. long; spikes solitary, closely flowered, 2 mm. thick × 6–10 cm. long, on axillary, 1-bracteate stalks; peduncle about 1 cm. long as represented; bracts round-peltate; fruit ellipsoidal, rostrate, stigma anterior at the base of the recurved beak.

Mountains of central Costa Rica and adjacent Panama.

CHIRIQUÍ: Boquete Region, Cerro Horqueta cloud forest, on fallen trees, alt. 1950 m., *von Hagen & von Hagen 2155*.

The specimen from Panama agrees in all essential characteristics with this species. The spikes are not fully developed and are somewhat fragmentary, but so far as can be determined they agree well with Trelease's description of those of *P. ciliifera*.

64. PEPEROMIA **conserta** Yuncker, sp. nov.

Herba glabra repens carnosa epiphytica; foliis alternis, ovato-ellipticis, apice acuminatis, basi rotundatis ex lamina 1–2 cm. peltatis, obscure palmatim 9-nerviis, sat conferte ciliatis, minute pellucido-punctatis; petiolo gracili; spicis terminalibus axillaribusque; drupa globoso-ovoidea rostrata.

A repent, spreading, epiphytic, glabrous herb; stem 3 mm. thick when dry, internodes up to 10 cm. or more long, rooting at the nodes; leaves alternate, ovate-elliptic, apex sharp-acuminate, base rounded, obtuse, peltate 1–2 cm. from the margin, 4–5 cm. wide × 6–8 cm. long, obscurely palmately 9-nerved, margin strongly ciliate, drying coriaceous, narrowly revolute, opaque, finely pellucid-dotted; petiole slender, variable in length, 4–10 cm. long; spikes terminal and axillary, 2 mm. thick × 8 cm. long, closely flowered; peduncle 10–15 mm. long; bracts small, round-peltate; fruit globose-ovoid, about 0.8 mm. long, rostrate, stigma anterior, near the base of the equilong, rather thick, granulate, curved,

blunt beak. — COLOMBIA: CAQUETÁ: Cordillera Oriental, in forest between Sucre and La Portada, alt. 1200–1350 m., April 5, 1940, *Cuatrecasas 9120* (Nat. Herb. Colombia, TYPE; fragment in U. S. Nat. Herb.).

Southern Colombia and Panama.

PANAMA: CHIRIQUÍ: Bajo Chorro, Boquete District, rain forest, alt. 1800 m., Jan. 10, 1938, *Davidson 85*.

So far as it has been possible to determine, the Panamanian specimen agrees in all essential characters with the one from Colombia.

65. PEPEROMIA MACULOSA (L.) Hook. Exot. Fl. 2:*pl. 92*. 1825.

Piper maculosum L. Sp. Pl. 1:30. 1753.
Peperomia variegata Ruiz & Pav. Fl. Peruv. & Chil. 1:33, *pl. 52, f. 2*. 1798.
Peperomia septuplinervia C.DC. in Jour. Bot. 4:142. 1866.
Peperomia monsterifolia Griseb. Cat. Pl. Cub. 64. 1866.
Peperomia leridana Trel. in Ann. Mo. Bot. Gard. 27:303. 1940.
Peperomia tenebraegaudens Trel. loc. cit. 305. 1940.
Peperomia Scheryi Trel. loc. cit. 28:426. 1941.

A rather large, sparingly hairy to glabrate, assurgent, succulent herb; stem spotted when growing, up to 10 mm. thick and ascending to 20 or 30 cm., rooting from the nodes of the decumbent basal part; leaves alternate, peltate within 1 cm. of the margin, elliptic-ovate, 6–11 cm. wide × 10–18 cm. long, apex abruptly short-acuminate, base rounded or truncately subcordate, rather faintly 7- to 11-plinerved below, or large leaves with as many more branches above the middle, drying dull and opaque, somewhat pubescent or glabrate; petiole 6–15 cm. long, fleshy, pubescent or glabrate; spikes terminal, solitary or paired, up to 25 cm. long; peduncle up to 5 cm. long, pubescent or glabrate; bracts round-peltate; fruit ellipsoidal, rostrate, stigma at the base of the curved beak.

West Indies, northern South America, and Panama.

CHIRIQUÍ: Finca Lérida to Boquete, alt. 1300–1700 m., *Woodson, Allen & Seibert 1176*; Bajo Mona, mouth of Quebrada Chiquero, along Río Caldera, alt. 1500–2000 m., *Woodson, Allen & Seibert 993*; Bajo Mona, Boquete District, alt. 1350 m., *Davidson 486*; forests around El Boquete, alt. 1000–1300 m., *Pittier 2984*; Quebrada Velo, alt. 1800 m., *Woodson & Schery 247*; Boquete, Boquete District, alt. 1140 m., *Davidson 727*.

All the specimens seen from Panama are less pubescent than those which have been examined from the West Indies and South America. *P. variegata* was described as glabrous and the Panamanian specimens agree in this particular. There is so much variation in this character among individual plants, however, that it does not appear advisable to base specific or varietal distinctions on it. It has been impossible to recognize *P. tenebraegaudens*, *P. Scheryi*, and *P. leridana* as distinct species, although they differ somewhat in the texture of the dried plants, leaf size, length of spikes, etc. None of these characters, however, appear sufficiently distinctive to warrant specific or varietal recognition. Field studies and mass collections are required to provide evidence for proper segregation of these questionable species, if such is indicated. All specimens seen from Panama are from an altitude of 1000–2000 meters in the mountains of Chiriquí.

66. PEPEROMIA **perglandulosa** Yuncker, sp. nov.

Herba epiphytica repens carnosa; caule conferte rubro-villoso; foliis alternis deltoideo-ovatis, apice rotundatis, basi truncatis, plerumque subpeltatis, palmatim 5-nerviis, supra glabratis subtus pubescentibus saltem ad costam conferte ciliatis utrinque conferte rubro-glanduloso-punctatis; petiolo 1.5–4 cm. longo conferte rubro-villoso, dissite rubro-glanduloso-punctato; spicis oppositifoliis; pedunculo 2.5 cm. longo conferte rubro-villoso ad medium bracteato; ovario ellipsoideo acute rostrato.

A repent, succulent, epiphytic herb; stem 2 mm. thick, densely red-villous, rooting at the nodes, internodes 2–5 cm. or more long; leaves alternate, deltoid-ovate, apex rounded, base truncate, mostly subpeltate with the petiole attached 1–2 mm. from the margin, palmately 5-nerved, the laterals slender and obscure, glabrescent above, pubescent beneath, at least along the midrib, the margin densely ciliate with a zone of submarginal hairs on the upper surface, 1.5–3 cm. wide × 1.5–3 cm. long, drying rather thick and opaque, densely and conspicuously red-glandular-dotted on both sides, the glands comparatively large; petiole 1.5–4 cm. long, densely red-villous, sparsely red-glandular; spikes leaf-opposed, 2 mm. thick × 7 cm. long, densely flowered; peduncle 2.5 cm. long, densely red-hairy, with scattered red glands, bracteate near the middle; floral bracts round-peltate, conspicuously and densely red-glandular; ovary ellipsoidal, red-glandular, sharply rostrate, stigma anterior at the base of the beak; fruit not present.

Known only from the type locality.

COCLÉ: El Valle de Antón, crest of Cerro Pajita, alt. 1100 m., Sept. 28, 1946, *Allen 3750* (Herb. Missouri Bot. Gard., TYPE).

The densely red-villous plants, and red-glandular leaves, bracts, etc. are distinctive features of this species.

VII. KEY TO SPECIES WITH NUMEROUS SPIKES ARRANGED IN A COMPOUND, PANICULATE INFLORESCENCE.

(Subgenus PANICULARIA Miq.).

a. Spikes scarcely more than 1 cm. long; fruit subcylindrical with oblique apex; inflorescence stalk microscopically hirtellous ..... 67. P. PERNAMBUCENSIS
aa. Spikes mostly 3 cm. or more long; fruit not as above.
b. Leaves sessile or subsessile ..... 68. P. DURICAULIS
bb. Leaves obviously petiolate.
c. Spikes mostly less than 10 in each panicle.
d. Leaves obovate, mostly 10 cm. or more wide ..... 69. P. WILLIAMSII
dd. Leaves elliptic-oblanceolate, scarcely 5 cm. wide.
e. Stems, leaves, etc. villous ..... 70. P. WEDELII
ee. Stems glabrous ..... 56b. P. OBTUSIFOLIA var. LONGIBRACTEATA
cc. Spikes mostly 12 or more in each panicle; leaves elliptic, elliptic-oblong, or oblanceolate, mostly 6–8 cm. wide.
d. Leaves glabrous; stem only a few cm. long, scarcely erect ..... 71. P. MAMEIANA
dd. Leaves pubescent, at least beneath.
e. Plants rhizomatous; leaves villous along the nerves beneath, glabrous above ..... 70. P. WEDELII
ee. Plants with erect stems up to 100 cm. tall; leaves silky-appressed-villous on both sides ..... 72. P. SUBSTRIATA

67. PEPEROMIA PERNAMBUCENSIS Miq. in Hook. Lond. Jour. Bot. 4:420. 1845.

Peperomia paniculata Regel, in Bull. Soc. Nat. Moscou 31:542, *pl. 3.* 1858.
Peperomia longifolia C.DC. in DC. Prodr. 16[1]:405. 1869.
Peperomia multiplex Leprieur ex C.DC. loc. cit. 406. 1869, as synonym.
Peperomia lopezensis Trel. in Ann. Mo. Bot. Gard. 27:303. 1940.

A simple, short-stemmed, succulent, terrestrial, or epiphytic herb; stem 3–5 mm. or more thick, ascending to 5–10 cm. from a briefly decumbent, rooting base, internodes very short, glabrous; leaves alternate, elliptic, elliptic-oblong, or oblanceolate, 4–6 or sometimes up to 12 cm. wide × 15–30 cm. long, apex sharp-acuminate, base cuneate, decurrent, pinnately nerved with 5–8 branches on each side of the prominent midrib, glabrous on both sides, minutely hirtellous at the tip, usually drying rather chartaceous and subopaque; petiole 3–5 cm. long; spikes about 2 mm. thick × 10–12 mm. long, verticillate in a loose, terminal or axillary, spike-like paniculate inflorescence up to some 8 cm. long, on a common stalk 4–8 cm. long, the main stalk of the panicle somewhat hirtellous or puberulent; peduncles about 3 mm. long; bracts round-peltate; fruit about 1 mm. long, subcylindrical, slightly obliquely truncate at the apex, stigma central.

Northern South America and extending into southern Central America.

BOCAS DEL TORO: Fish Creek Mountains, vicinity of Chiriquí Lagoon, *von Wedel 2253, 2286.* CANAL ZONE: Quebrada Lopez, *Allen 2118.*

The leaves on the specimens seen from Panama are somewhat more elongated than most of those seen from South America and consequently do not appear as abruptly acuminate. This character which, so far as has been noted, is not supported by other differences, does not appear to be sufficient to warrant the maintenance of *P. lopezensis* as a distinct species.

68. PEPEROMIA DURICAULIS Trel. in Ann. Mo. Bot. Gard. 27:302. 1940.

An erect or assurgent, glabrous, leafy, terrestrial or epiphytic, alpine herb; stem 5 mm. thick downward when dry, ascending to 20–30 cm., internodes 1–3 cm. long, nodes rather prominent; leaves alternate, elliptic-oblanceolate, apex sharp-acuminate, minutely hirtellous, base cuneate-decurrent, 3–4.5 cm. wide × 10–13 cm. long, pinnately nerved, the nerves 5–6 on each side of the prominent midrib, drying submembranous, translucent, faintly but densely pellucid-dotted; petiole very short, broadly winged to the base by the decurrent blade, the wings clasping the stem; spikes 1 mm. thick × 3–5 cm. long, in umbels of usually 3–5 spikes in the axil of a lanceolate bract, the umbels alternately arranged in an open, divaricate, paniculate, axillary inflorescence eventually up to 15 cm. or more long, the basal part to the first umbel up to 7 cm. long in anthesis; peduncle of individual spike 5–10 mm. long; floral bracts round-peltate; fruit ellipsoidal, rostrate, stigma at the base of the elongate beak.

Southwestern Panama.

CHIRIQUÍ: trail from Cerro Punta to headwaters of Río Caldera, alt. 2250–2500 m., *Allen 1441;* Bajo Chorro, Boquete District, alt. 1800 m., *Davidson 299.*

69. Peperomia Williamsii Trel. in Contr. U. S. Nat. Herb. 26:48. 1927.

Peperomia flavispica Trel. loc. cit. 1927.

A glabrous, succulent, subsimple, arboricolous herb; stem up to 1 cm. thick when dry, rather short, internodes 2–3 cm. long; leaves alternate, elliptic-obovate, apex rounded, obtuse, or abruptly acute, commonly emarginulate, base cuneate, decurrent, 9–11 cm. wide × 15–20 cm. or more long, pinnately nerved to above the middle, the lateral nerves very slender, about 6 on each side, drying thick, glossy, coriaceous, opaque, subrevolute; petioles stout, 5–12 cm. long, winged by the decurrent blade; spikes 2 mm. thick × 10–15 cm. long, closely flowered, several, solitary, or 2 or 3 from the nodes of a zig-zag, elongated stalk-like continuation of the stem, inflorescence up to 15 cm. or more long; peduncles of individual spikes 2–4 cm. long; rachis with anastomosing ridges; bracts round-peltate; fruit ellipsoidal, about 1 mm. long, rostrate, stigma at the base of an awl-like, equilong beak with hooked apex.

Panama.

COCLÉ: Bismarck, above Penonomé, alt. 600–900 m., *Williams 433*. CANAL ZONE: Las Cascadas Plantation, near Summit, *Standley 25729*; drowned forest near Vigia and San Juan on Río Pequení, alt. 66 m., *Dodge, Steyermark & Allen 16525*—leaves 5–7 × 12–15 cm. PANAMÁ: Río Tapia, *Standley 26196*.

The large, succulent, obovate leaves with stout petioles and paniculately clustered spikes are distinctive features of this species. No specific differences have been noted between this species and *P. flavispica*.

70. Peperomia **Wedelii** Yuncker, sp. nov.

Fig. 23. *Peperomia Wedelii*

Herba subrepens rhizomatosa epiphytica; caule dissite villoso, indumento ad 1 mm. longo, internodiis brevibus; foliis alternis oblanceolato-ellipticis, apice breviter acuminatis, basi cuneatis, pinnatim venosis, venis utrinque ca. 5, supra glabris subtus ad venas dissite villosis; petiolo 1–3.5 cm. longo, dissite villoso; spicis in paniculam terminalem dispositis; pedunculo ca. 1 cm. longo glabro; drupa angustata erecta oblongo-cylindrica rostrata.

A subrepent, rhizomatous, epiphytic herb; stem 2 mm. thick when dry, loosely villous, hairs up to 1 mm. long, internodes short; leaves alternate, oblanceolate-elliptic, apex short-acuminate, base cuneate-decurrent, 3–5 cm. wide × 10–15 cm. long, pinnately nerved, the lateral nerves about 5 on each side, glabrous above, loosely villous along the nerves beneath, drying rather

papery, translucent; petiole 1–3.5 cm. long, loosely villous, shallowly grooved above; spikes 1 mm. thick × 3–6 cm. long, single or 2–3 in alternate clusters in an elongated terminal panicle, the lowermost spikes about 7 cm. above the base of the loosely villous stalk; peduncles of individual spikes about 1 cm. long, glabrous; floral bracts minute, round-peltate; fruit slender, erect, oblong-cylindrical, rostrate, stigma anterior at the base of the short, flexible beak.

Known only from the type locality.

BOCAS DEL TORO: Fish Creek, vicinity of Chiriquí Lagoon, April 9, 1941, *H. von Wedel 2005* (Herb. Missouri Bot. Gard., TYPE).

This species appears to be rather closely related to *P. calvifolia* of Costa Rica. It differs, however, in the pubescence of the stem, leaves, etc., fewer lateral leaf nerves, longer petioles and spikes, etc.

71. PEPEROMIA MAMEIANA C.DC. in Candollea 1:290, 396. 1923, as *P. mamaiana* C.DC. in Candollea 2:188. 1925.

A glabrous, rather succulent, rhizomatous herb, on rocks and trees; stem 4–8 mm. thick when dry, rooting at the nodes, internodes 1–2 cm. long; leaves alternate, elliptic, lance-elliptic, or suboblanceolate, apex acute, base cuneate-decurrent, 4–10 cm. wide × 15–25 cm. long, obscurely pinnately nerved, the nerves 6–7 on each side of the stout midrib which continues to the very apex, drying rather glossy, coriaceous, opaque, narrowly revolute; petiole stout, up to 10 cm. long, channelled and winged upward by the decurrent blade; spikes 1–1.5 mm. thick × 6–12 cm. long, densely flowered, loosely paniculate on long, stout, axillary or terminal stalks, the entire inflorescence up to 30 cm. or more long; peduncles 1–5 cm. long; rachis with anastomosing ridges; bracts round-peltate; fruit scarcely 1 mm. long, ellipsoidal, rostrate, stigma anterior at the base of the curved beak.

Central Panama.

CANAL ZONE: Mamei Hill, alt. 20–90 m., *Pittier 3805;* vicinity of Las Cruces, alt. 26–40 m., *Seibert 571;* Barro Colorado Island, *Kenoyer 303;* near Salamanca Hydrographic Station on the gorge of the Río Pequení, alt. 70–80 m., *Dodge, Steyermark & Allen 16525a;* Experimental Gardens, *Lindsay 402a.*

72. PEPEROMIA SUBSTRIATA C.DC. in Candollea 1:291. 1923.

A moderately large herb; stem somewhat silky-pubescent, erect or scandent, rooting at the nodes, with erect branches, up to 5 mm. thick when dry, internodes up to 7 cm. or more long; leaves alternate, elliptic, apex short-acuminate, base acute, 2–4 cm. wide × 4.5–8 cm. long or up to 6.5 × 16 cm., pinnately nerved nearly throughout, the lateral nerves 6–8 on each side, appressed silky-villous on both sides, drying rather thick, opaque; petiole up to 6 cm. long, moderately appressed silky-villous, channelled and narrowly winged; spikes 2 mm. thick × 6–10 cm. long, closely flowered, several on a bracted, silky-villous stalk 3 cm. or more long; bracts large, foliar, elliptic-obovate, sparingly silky; peduncle of indi-

vidual spikes 5–10 mm. long; floral bracts round-peltate, glandular-dotted; fruit ellipsoidal, about 1 mm. long, rostrate, stigma anterior near the base of the beak.

Costa Rica and adjacent Panama.

BOCAS DEL TORO: Robalo Trail, northern slopes of Cerro Horqueta, alt. 1800–2100 m., *Allen 4950*. CHIRIQUÍ: Bajo Chorro, Boquete District, rain forest, alt. 1800 m., *Davidson 217*.

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Robert E. Woodson, Jr., Robert W. Schery and Collaborators 121–314

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FLORA OF PANAMA

Part V. Fascicle 2

RESEDACEAE

A small family of annual or perennial herbs with alternate or fasciculate leaves and spicate racemes of small, asymmetrical flowers with white or yellowish, cleft petals. No genera or species are indigenous to the New World, most of them being native to the Mediterranean area. The genus *Reseda* ("mignonette", *reseda*) has been introduced into Panama and is cultivated in gardens in the Boquete region.

MORINGACEAE

This family, consisting of a single genus and very few species, is represented in Panama by *Moringa oleifera* Lam., which has been introduced into cultivation from the Old World tropics. The plants are shrubs or small trees with brittle, rather resinous or gummy branches, and whitish bark. The leaves are large, alternate, and twice or thrice pinnate. The inflorescence is paniculate and axillary with rather mediocre but fragrant, white or reddish flowers. The fruit is a rather large and elongate, 3-angled capsule dehiscent by three valves; the seeds are 3-winged and oily.

The vernacular name of *M. oleifera* is "horseradish tree" or *marango*, a name arising from the flavor and odor of the roots. The oil from the seeds is comestible or may be used as a substitute for ben oil which is produced as a lubricant for watches and other delicate mechanisms from a related species, *M. aptera*.

CRASSULACEAE

Usually fleshy or succulent herbs or subshrubs, with thick stems and alternate (infrequently opposite), many-ranked leaves. Leaves usually thick and fleshy, mostly simple and entire or crenulate, infrequently pinnately compound, in many species living for a considerable time after being removed from the plant and in some cases capable of producing plantlets from the marginal indentations. Inflorescence frequently cymose, less often racemose or paniculate. Flowers typically coarse and stiff, perfect, regular, polypetalous or sympetalous; calyx 4- to 5-parted, the sepals free or united; petals 4–5, free or united, mostly persistent; stamens in 1 or 2 cycles, each cycle isomerous with the petals; carpels as many as the petals or sepals, essentially free or united at the base, the ovules usually numerous from a ventral placenta; receptacle normally with a scale opposite each carpel. Fruit follicular from the individual carpels; seeds small, punctulate.

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A family represented in almost all parts of the world, especially in Africa; best represented in warmer latitudes, not uncommonly under subalpine conditions. A. Berger (in Engl. & Prantl, Nat. Pflanzenfam. 18a:352–483. 1930) probably has given the most acceptable recent treatment of the family.

a. Tall herbs; leaves opposite, petiolate, often pinnate; flowers 4-merous, the calyx tubular, inflated..... 1. Bryophyllum
aa. Small herbs; leaves spiral, sessile, simple; flowers 5-merous, the sepals essentially free..... 2. Echeveria

1. BRYOPHYLLUM Salisb.

Bryophyllum Salisb. Parad. Londin. *pl. 3*. 1805.

Physocalycium (?) Vest, in Flora, III, 2:409. 1820.
Crassouvia Commers. ex DC. Prodr. 3:395. 1828.
Kalanchoe R. Hamet, in Bull. Herb. Boiss. II, 7:870. 1907, in part.

Erect, succulent, perennial herbs or subshrubs, usually glabrous. Leaves mostly simple but sometimes pinnately compound, opposite, thick and fleshy. Inflorescence usually a terminal panicle. Flowers perfect, regular, usually nodding, mostly 4-merous; sepals 4; usually united into an inflated tube; petals 4, sympetalous, somewhat exceeding the calyx, usually constricted above the ovary, the lobes shorter than the tube; stamens inserted on the lower corolla tube, the filaments about equalling the corolla; carpels partly united or distinct; ovules numerous; disc bearing 4 glands or scales. Fruit normally of 4 follicles.

The genus is distinguished from the New World genera of the family in possessing the large, inflated calyx and opposite, sometimes compound leaves. It resembles the African and Asian genera *Kalanchoe* and *Kitchingia*, differing from these in the insertion of the stamens toward the base of the corolla tube in the large, nodding flowers. A single species is naturalized widely in Panama, but is not frequently collected.

1. Bryophyllum pinnatum (Lam.) S. Kurz, in Jour. Asiatic Soc. Bengal 40^2:52. 1871.

Cotyledon pinnata Lam. Encycl. Meth. 2:141. 1786.
Calanchoe pinnata Pers. Syn. Pl. 1:446. 1805.
Bryophyllum calycinum Salisb. Parad. Londin. *pl. 3*. 1805.

Perennial, little-branched herb as much as 1 m. tall or taller, the stems fleshy, glabrous, lustrous, the roots diffuse. Leaves opposite, simple or less frequently 3- to 5-pinnate (usually both simple and pinnate leaves on the same plant), in compound leaves the terminal leaflet the largest; blade of leaf or leaflets oblong, rounded at base and apex; coarsely crenate, glabrous, as much as 13 cm. long and 7 cm. broad, fleshy and obscurely nerved, capable of producing plantlets from the indentations of the leaf margin; petiole conspicuous, commonly 3–4 cm. long on older leaves, fleshy, glabrous, widened toward the base, exstipulate but with decurrent interpetiolar lines on the subtending internode. Inflorescence a glabrous, terminal, thrice-compound panicle as much as 5 dm. long, the bracts and bractlets

minute and caducous. Flowers large and conspicuous, with pedicels mostly about 1 cm. long; calyx broadly tubular, inflated, usually about 3 cm. long and 1 cm. broad, 4-lobed for one-fourth or one-fifth its length, greenish often tinged reddish; corolla tubular, 4–5 cm. long, mostly enclosed by the calyx, markedly constricted just above the ovary and thence ventricose, 4-lobed, the lobes triangular and acuminate, glabrous, reddish; stamens 8, inserted at the base of the corolla tube, the filaments almost as long as the corolla.

Native of tropical Africa and Madagascar; introduced and naturalized in the tropics throughout the world.

CHIRIQUÍ: Boquete, *Woodson & Schery 759.*

The species is quite common in the American tropics, both as a cultivated plant and as an escape. The rather bizarre flowers are not unattractive and the peculiar ability to produce plantlets at the notches of the leaves enhances its interest, earning the popular names "life plant" and *hoja del aire.* Standley reports (Fl. Panama Canal Zone, p. 187. 1928): "Among the West Indians of the zone [Canal Zone] a favorite method of testing the fidelity of a sweetheart is to place a leaf of this plant above one's door. If a new plant is produced at each notch, her faithfulness can not be questioned."

2. ECHEVERIA DC.

ECHEVERIA DC. Prodr. 3:401. 1828.

Caulescent or scarcely stemmed perennial herbs, the leaves frequently borne in a basal rosette, fleshy and succulent. Leaves spirally arranged, sessile, entire, usually glabrous and somewhat glaucous. Inflorescence usually a lax spike or raceme, the flowers arising singly or in pairs in the axils of the reduced stem-leaves. Flowers fleshy, variously colored; sepals 5, more or less free, equal or unequal, frequently erect, mostly greenish; petals 5, usually exceeding the sepals, free or somewhat united at the base, frequently erect and angled; stamens 10, the outer cycle mostly inserted at the base of the petals; carpels 5, united at the extreme base, tapered into slender styles. Fruit follicular.

An interesting and attractive genus much used for ornamentals because of the rosettes of thick, handsome foliage. Distinctive characters frequently are lost in making herbarium sheets of such succulents, which may account for the widespread confusion of species limits. Horticulturalists have been particularly concerned with the difficulty in naming specimens accurately, and such students of the group as Britton and Rose (N. Am. Fl. 22:13–26. 1905) and von Poellnitz (Fedde Rep. Spec. Nov. 39:193–270. 1936) apparently have overdone the splitting of species.

The genus occurs in the southern United States to middle South America, centering in Mexico. A single species is known to occur in Panama.

1. ECHEVERIA AUSTRALIS Rose, in Bull. N. Y. Bot. Gard. 3:6. 1903.

Caulescent, little-branched, succulent herb to a few decimeters tall, glabrous and more or less glaucous. Leaves sessile, obovate or spatulate, up to 7 cm. long

and almost 3 cm. broad in the larger, basal leaves, progressively smaller along the flowering stems, rounded or abruptly acute at the tip, broadly cuneate at the base, entire. Inflorescence terminal, appearing racemose by the insertion of flowers in the axils of reduced, frequently caducous leaves; pedicels 2–5 mm. long. Flowers moderate, pink; sepals 5, narrowly or broadly ovate, rather unequal, 5–10 mm. long; petals 5, lanceolate, about 1 cm. long, rather thick and rigid, mucronate-acute, essentially free; stamens 10, almost equalling the petals; filaments slender, glabrous; anthers oblong, about 1 mm. long.

Costa Rica and Panama.

CHIRIQUÍ: Río Chiriquí Viejo valley, *P. White 39*.

PODOSTEMONACEAE

By P. VAN ROYEN

Small, usually matted herbs growing in rapids and waterfalls, flowering when the water subsides seasonally, very variable in size, the smaller ones thalloid and closely adhering to the supporting rocks, the larger ones with distinct stems often arising in pairs from long and thin roots, in other instances rootless; sterile plants often larger and coarser than the fertile ones. Leaves alternate, di- or tristichous, in the stemless species sometimes united at the base and springing in 2 rows from an irregular base, entire or much divided, sometimes with bundles of minute threads on one or both sides; stipule 1, a sheath and a ligula sometimes present. Flowers solitary or fascicled between the leaf-bases or at the ends of short branches or in distinct inflorescences, hermaphrodite, actinomorphic or zygomorphic, the younger ones enveloped by a thin spathe or by a few leaves. Tepals 2 to many, distinct or reduced to minute scales, free or united. Stamens 1 to many, alternate with the tepals in a complete or incomplete whorl, free or united to the tepals; anthers sagittate, 4–celled, dehiscing by 2 longitudinal slits, introrse or extrorse, dorsi- or basifixed; pollen 1- or 2-celled. Ovary superior, sometimes oblique or nearly perpendicular to the (frequently) distally enlarged pedicel, 2- or 3-, or sometimes 1-celled; carpels equal or unequal, ribbed or smooth without, the placenta axile, fleshy, with 2 to numerous anatropous ovules; ovules with 2 integuments; styles 2–3, free or cohering, each with a distinct stigma. Fruit dehiscing septifragal with 2 or 3 valves, in fruits with unequal cells the smallest valve sometimes soon falling off; seeds 2 to many, without endosperm.

About 200 species distributed in the tropics throughout the world, ascending the southern Appalachian Mountains in the southeastern United States.

a. Flower buds enclosed between a few leaves; perianth distinct; ovary 3-celled; leaves entire ..... 1. Tristicha
aa. Flower buds enclosed in a membranaceous spathe; perianth reduced to minute scales; ovary 2-celled; leaves much divided ..... 2. Marathrum

1. TRISTICHA Du Petit Thouars

TRISTICHA Du Petit Thou. Gen. Nov. Madagasc. 2. 1806.

Dufourea Bory, ex Willd. Sp. Pl. 5:55. 1810.
Philocrena Bong. in Mem. Acad. Sci. St. Petersb. VI, 3^2:80–82. 1835.
Potamobryon Liebm. in Forhandl. Skand. Naturf. Kjoeb. 5:512. 1847.

Moss-like herbs widely differing in shape and size, much branched, forming dense mats on rocks; stems thin, terete. Leaves tristichous, the rows in the older plants sometimes indistinct, entire, membranaceous, nerved or unnerved, the apex obtuse or acute, often divided into 2 or 3 parts in older leaves. Flowers terminal or on short side-branches, enclosed between 2–3 distinctly larger leaves when young; perianth well-developed, membranaceous, 3-partite, marcescent; stamen 1, the filament slender, the anther ovate, introrse, with elongate connective, the pollen globose; ovary 3-celled, with 3 equal carpels, ovoid to subglobose, rounded or attenuate at the base, the placentas swollen, dehiscing with 3 equal valves each with 3 ribs; seeds numerous.

Tropical and subtropical America, Africa, and Asia.

Fig. 54. *Tristicha trifaria*

1. TRISTICHA TRIFARIA (Willd.) Tul. in Arch. Mus. Hist. Nat. 6:179–189. 1852; Warming, Fam. Podost. 6:28–30, *f. 24.* 1901.

Dufourea trifaria Willd. Sp. Pl. 5:55. 1810; in Mag. Ges. Naturf. Fr. Berlin 5:63–64. 1811.
Dufourea hypnoides St. Hil. in Mem. Mus. Paris 10:472. 1823.
Tristicha hypnoides (St. Hil.) Spreng. Syst. Veg. 4^2:10. 1827; Cario, in Bot. Zeit. 39:25, *tab. 1–24.* 1881.
Dufourea Boryi A. Rich. in Chev. Dict. Drogues 5:636. 1829.
Philocrena pusilla Bong. in Mem. Acad. Sci. St. Petersb. VI, 3^2:80, *tab. 6.* 1835.

Potamobryon concinnum Liebm. in Forhandl. Skand. Naturf. Kjoeb. 5:513. 1847.
Potamobryon laxum Liebm. loc. cit. 514. 1847.
Potamobryon patulum Liebm. loc. cit. 515. 1847.
Tristichia concinna (Liebm.) I. M. Johnston, in Sargentia 8:130. 1949.

Small herbs with shoots forming dense mats attached to much-branched roots; stems terete, 0.2–9.0 cm. long. Leaves tristichous, the rows at first regularly alternating with one another, the older leaves in irregular whorls of 3–6; one row always on the dorsal side of the stem, these ovate, 0.5 mm. wide to 1 mm. long; the other two rows lateral and at the same level, obliquely inserted, these spathulate, to 1 mm. wide, to 3 mm. long; all leaves definitely nerved, entire, obtuse, sessile, sometimes all alike or the older with 2–4 acute apices; fertile branches with 2–3 membranaceous leaves 2.0–2.5 mm. long, which enclose the young flower. Perianth 3-fid or -partite, the lobes obtuse, nerved, 1–2 mm. long; stamen 1.5–2.5 mm. long, the filament spathulate, distinctly nerved, 1–2 mm. long, the anther sagittate or ovate, truncate, slightly emarginate at the base, about 0.8 mm. long; pollen globose, 16–17 μ in diameter, yellowish; ovary ellipsoid, roundish or attenuate at the base, 0.5–1.0 mm. long, about 0.8 mm. in diameter; styles 3, linear, about 0.5 mm. long, often papillate; pedicel 3–15 mm. long, terete.

Widespread in Central and South America, Cuba, and Africa.

CANAL ZONE: Río Pedro Miguel, *Standley 29933, 29934;* Río Paraiso, *Standley 29878;* Quebrada Ancha, *Steyermark & Allen 17130;* Las Cascadas, near Summit, *Dodge & Hunter s. n.;* Río Boquerón, *Steyermark & Allen 17257;* Río Indio, *Dodge & Allen 17400.*

2. MARATHRUM Humb. & Bonpl.

MARATHRUM Humb. & Bonpl. Pl. Aequinox. 1:40–41, *tab. II.* 1808.

Lacis Mart. Nov. Gen. & Sp. 1:6. 1824.

Small to medium-sized stemless herbs known to be attached to roots in only a few species, the sterile plants often larger and coarser than the fertile, with an irregular, sometimes branched, adhesive base. Leaves either distichous or inserted along the margin of the thalloid base, repeatedly pinnate with all the pinnae alternate or slightly opposite, or entire with a few lobes along the margin; petiole sometimes fleshy, often dilated at the base. Flowers at first enclosed in a persistent, membranaceous spathe which splits irregularly at the tip, 1 to many, solitary or fascicled between the leaf-bases; pedicel scarcely enlarged at the tip in some speciès, in others abruptly enlarged; tepals 3–25 in a complete or incomplete whorl, inconspicuous, squamiform to filiform, inserted on the margin of the receptacle in species with enlarged pedicels, but sometimes inserted at different levels in species with normal or scarcely enlarged pedicels; stamens 2–25, in a complete or incomplete whorl (the latter unknown in Panamanian species), rarely united at the base, the filaments lanceolate, 3-angled at the base, sometimes branched, nerved, the anthers sagittate, introrse; pollen ellipsoidal to subglobose, 3-sulcate; ovary 2-celled, ellipsoidal, attenuate at the base, with 2 equal carpels, 8-ribbed; placenta

of the same shape as the ovary, with many ovules; styles 2, filiform or cylindric, cohering at the base or very rarely free, often emarginate. Fruit with 2 equal, persistent, 5-ribbed valves.

Central America, Antilles, northwestern South America.

a. Pedicels not thickened at the tip; leaves 3–5 times pinnate.
  b. Stamens one-third to one-half as long as the ovary; pollen ellipsoidal, 17 × 14 μ ..... 1. M. STENOCARPUM
  bb. Stamens about as long as the ovary.
    c. Tepals 0.5–1.0 mm. long; styles 2–3 mm. long; pollen ellipsoid, 16 × 13 μ ..... 2. M. OXYCARPUM
    cc. Tepals 0.5 mm. long or shorter; styles 0.5–2.0 mm. long.
      d. Leaves shorter than 3 cm., usually some dilated and cuneately fasciate-flabelliform; pollen subglobose, 15 × 14 μ ..... 3. M. PUSILLUM
      dd. Leaves 0.5–20 cm. long, of essentially similar form throughout.
        e. Ultimate leaf-divisions filiform or nearly so.
          f. Leaf rachis not winged, transparent when young; pollen narrowly ellipsoid, 20 × 11 μ; styles 0.5–1.0 mm. long ..... 4. M. LEPTOPHYLLUM
          ff. Leaf rachis distinctly winged, not transparent when young; pollen ovoid, 16 × 14 μ; styles 1.0–2.0 mm. long ..... 5. M. INDIFFERENS
        ee. Ultimate leaf-divisions usually round to spathulate or triangular, not filiform.
          f. Leaf rachis narrowly winged; ovary 2.5–3.0 mm. long; pollen subglobose, 15 × 14 μ ..... 6. M. CHEIRIFERUM
          ff. Leaf rachis not winged; ovary 3.5–4.0 mm. long; pollen ellipsoid, 17 × 14 μ ..... 7. M. ALLENII
aa. Pedicels thickened at the tip; leaves repeatedly bifurcate ..... 8. M. FOENICULACEUM

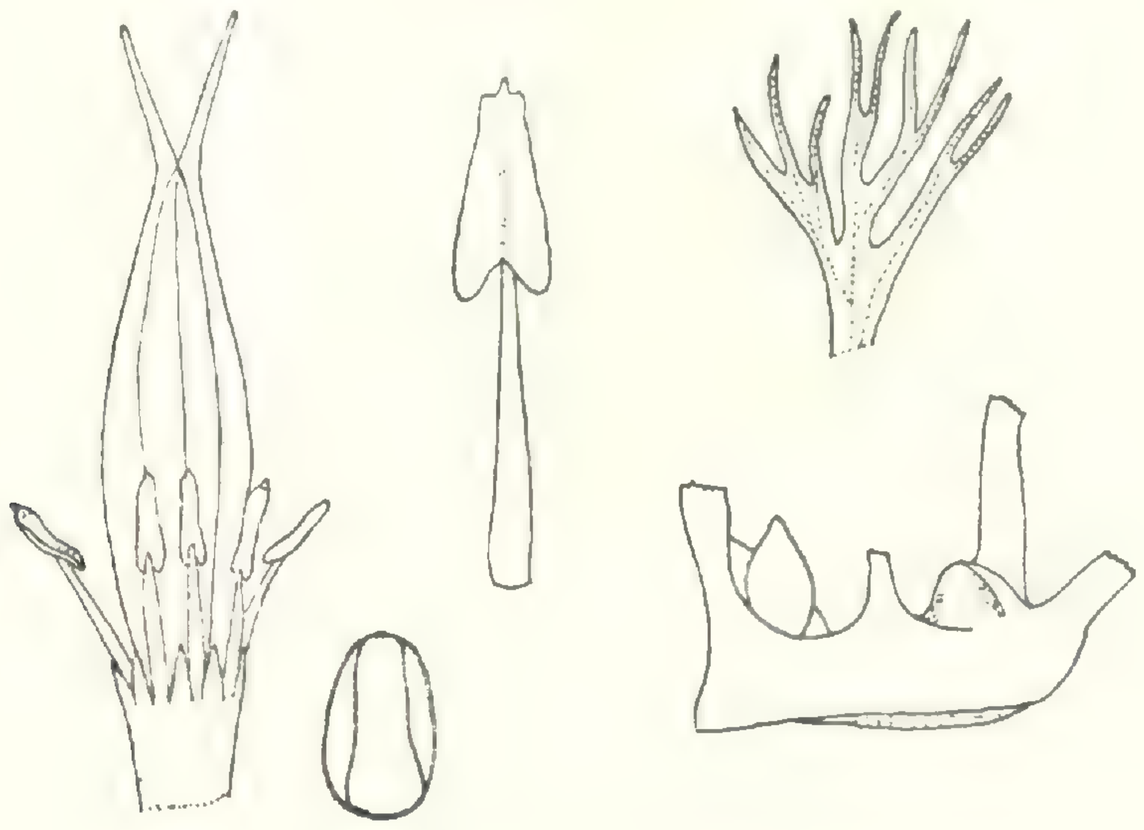

Fig. 55. *Marathrum stenocarpum*

1. MARATHRUM **stenocarpum** (Wedd.) v. Royen, comb. nov.

Marathrum Schiedeanum (Cham.) Tul. var. *stenocarpum* Weddell, in DC. Prodr. 17:54. 1873.

Small to medium-sized herbs; base cuneiform to more or less discoid, 1–2 cm. wide, 1–3 cm. high. Leaves 3 times pinnate, 3–20 cm. long, all the pinnae ascending at an angle of about 45°; primary pinnae 0.5–5.0 cm. long, 2–15 cm. apart; secondary pinnae 1–7 mm. long, 2–5 mm. apart; tertiary pinnae repeatedly forked,

Fig. 56. *Marathrum oxycarpum*

the ultimate divisions to 1 mm. long and 0.3 mm. wide, spathulate, acute, mostly nerveless; petiole 0.5–8.0 cm. long, 1–2 mm. wide, flattened, membranaceously dilated at the base and with a more or less distinct, obtuse, membranaceous ligula 1.0–1.5 mm. long. Flowers few, solitary; pedicel 1–4 cm. long; young spathe clavate, acute, 1.0–1.25 mm. long, the older infundibuliform, 3–5 mm. long; tepals 9, lanceolate, acute, nearly 1 mm. long; stamens 9, 1.5–2.0 mm. long, the filaments lanceolate, about 1.5 mm. long, the anthers obtuse, nearly 1 mm. long; pollen ellipsoidal, 17 × 14 μ, the lobes tapering toward one of the poles; ovary narrowly ellipsoid, acute, attenuate at the base, with 6 indistinct and 2 more distinct ribs marking the sutures, 3.5–4.0 mm. long, the styles 2, cylindrical, 3-edged at the base, the narrow wings passing into the midribs of the valves, papillate at the apex only, about 1.5 mm. long. Fruit with 2 distinctly 5-ribbed valves.

Panama and Colombia.

PANAMÁ: Juan Díaz River, *Killip 3390*. CANAL ZONE: Río Boquerón, *Steyermark & Allen 17255*.

2. MARATHRUM OXYCARPUM Tul. in Ann. Sci. Nat. III, 11:94. 1849.

Medium-sized herbs; base 2.5–30.0 mm. long, 2–8 mm. wide. Leaves 3 times pinnate, 3–50 cm. long, with all the pinnae alternate and ascending at an angle of 30–60°; primary pinnae 0.3–9.0 cm. long, 0.2–3.0 cm. apart; secondary pinnae 0.1–2.5 cm. long, 0.5–7.0 mm. apart, sometimes subopposite; tertiary pinnae 3–10 mm. long, 1–2 mm. apart, alternately pinnate with forked lobes, the ultimate divisions spathulate, acute, nerveless, rarely distinctly nerved, to 3 mm. long and 0.3 mm. wide; petiole flattened, slightly ribbed, membranaceously widened, 0.3–12.0 cm. long, 0.5–4.0 mm. wide; rachis straight, with an obtuse membranaceous ligule about 2 mm. long. Flowers solitary; pedicel 4–9 cm. long; young spathe clavate, acute, 2–5 mm. long, the older infundibuliform, 8–10 mm. long; tepals 8–10, triangular, acute, 0.5–1.0 mm. long; stamens 8–10, 5–6 mm. long, the filaments lanceolate, membranaceous, somewhat scaphiform at the base, 4.0–4.5 mm. long, the anthers obtuse, 1–2 mm. long; pollen ellipsoidal, 16 × 13 μ, the lobes tapering toward one of the poles; ovary ellipsoid, acute, base attenuate, flattened, 3.5–5.0 mm. long, 1.5–2.0 mm. wide, ribs 8, distinctly raised, the styles filiform, with widened sometimes emarginate apex, 2–3 mm. long. Fruit with 2 equal, distinctly 5-ribbed valves.

Honduras, Panama, and Colombia.

COCLÉ: Penonomé, *Williams 371*. PANAMÁ: Río Sta. Maria, *Seemann 34*.

3. MARATHRUM **pusillum** v. Royen, sp. nov.

Herbae pusillae. Folia pinnata; pinnis primariis fere 8 pro folio, interdum ala lata ad rhachem decurrente; pinnis secundariis interdum subopppositis; pinnis tertiariis repetito furcatis; laciniis ultimis lanceolatis, acutis, enerviis, 0.5–2.0 mm. longis; incisionibus obtusis. Flores 1–3, solitarii vel fasciculati; pedicello apice non dilatato; spathella juvenile clavata, acuta, vetusta infundibuliforme; tepalis 7, squamiformibus; staminibus 7, filamentis lanceolatis basi triangulare; antheris obtusis, emarginatis vel mucronatis; granulis pollinis subglobosis; ovario ovoideo, acuto, basi attenuato, valde applanato, distincte 8-costato, costis paulo prominentibus, duobus eorum indistinctissimis; stylis cylindricis, apice oblique truncatis, facie interne emarginatis, aliquando papillatis. Fructus valvis 2 aequalibus, utraque valva 5-costata.

Small species with base 1–4 mm. long and wide, 1–2 mm. thick. Leaves pinnate, 0.5–2.5 cm. long; primary pinnae about 8 per leaf, 1–7 mm. long, sometimes with a broad wing running down the rachis; secondary pinnae 0.5–2.5 mm. long; tertiary pinnae repeatedly forked, 1.0–2.5 mm. long, the ultimate divisions lanceolate, acute, nerveless, to 2 mm. long, the incisions obtuse. Flowers 1–3, solitary or in small groups; pedicel 0.7–2.0 cm. long; young spathe clavate, acute, splitting at the top or side, 1.5–3.0 mm. long, the older infundibuliform, 4–5 mm. long; tepals 7, squamiform, about 0.3 mm. long; stamens 7, about 3.5 mm. long,

Fig. 57. *Marathrum pusillum*

filaments lanceolate, 3-sided at the base, about 2.5 mm. long, anthers 1.0–1.5 mm. long, obtuse, emarginate or mucronate, the thecae unequal; pollen subglobose, about 15 × 14 μ; ovary ovoid, acute, base attenuate, strongly flattened, with 8 very slightly raised ribs (2 of them very indistinct), 2.0–2.5 mm. long, about 1 mm. wide, the styles cylindrical, apex obliquely truncate, emarginate at the inner side, slightly papillate, 1.5 mm. long. Fruit with 2 equal 5-ribbed valves. Leaves sometimes with a dilated and cuneately fasciate-flabelliform rachis about 1 cm. long and 2–3 mm. wide at the tip and there with 3–5 lobes with ultimate divisions as described above.

PANAMÁ: Chagres River, *Pittier 2303* (HOLOTYPE in U. S. Nat. Herb.).

This species is recognized easily by its size, since it is the smallest *Marathrum* ever found. The cuneate leaves, which are often on the same specimen with the normal leaves, are characteristic, too, and by these leaves the plants are different from all other Marathrums.

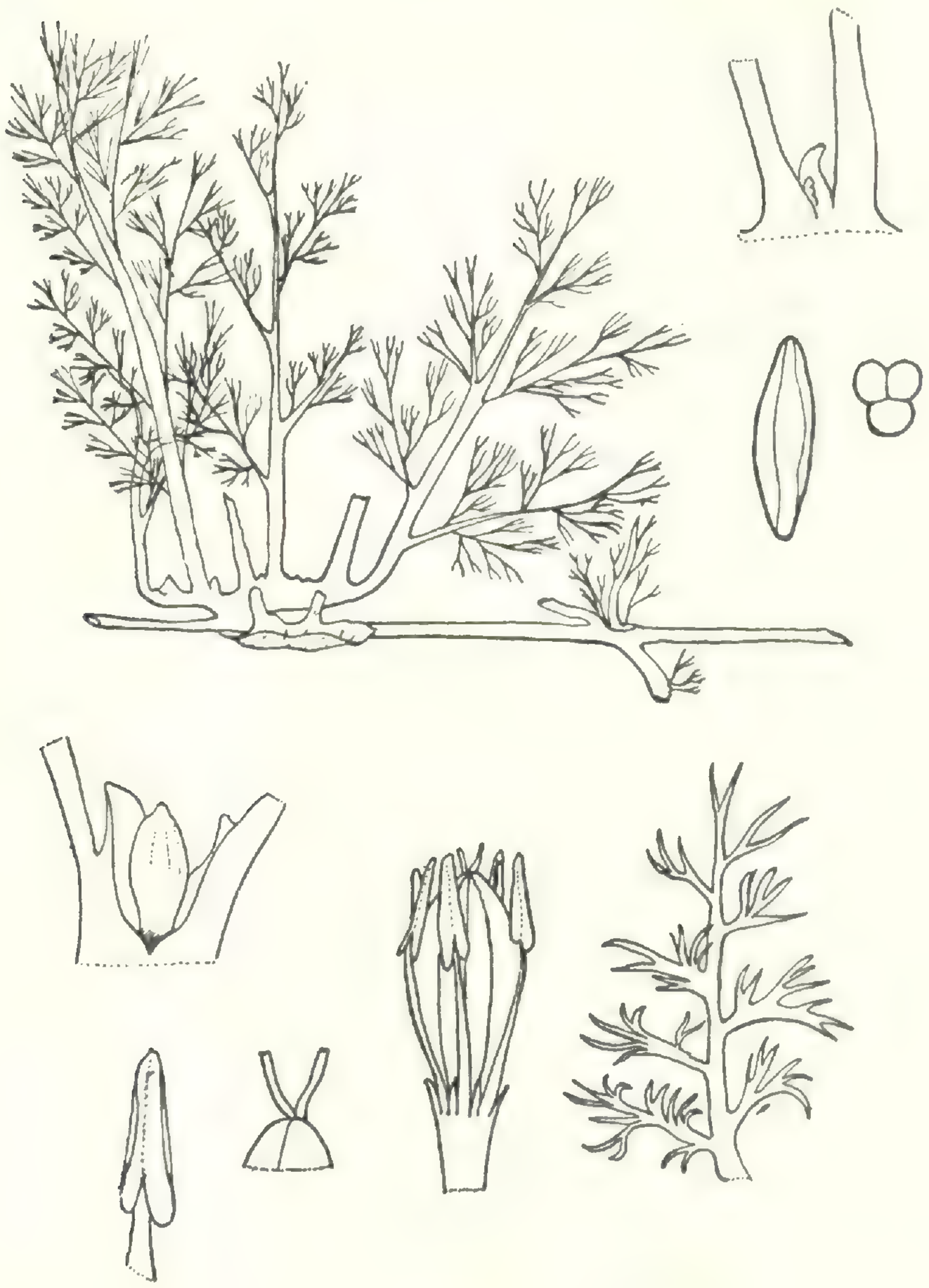

Fig. 58. *Marathrum leptophyllum*

4. MARATHRUM **leptophyllum** v. Royen, sp. nov.

Herbae parvae, acaules e radicibus longis, tenuibus appalantisque binatim nascentes. Folia tenuia, 3- vel 4-tim pinnata; petiolo juventate hyalino, interdum brevi tenui ligula 1 mm. alta instructo; pinnis primariis pinnatis vel bifurcatis; pinnis tertiariis repetito bifurcatis, laciniis ultimis lanceolatis, subfiliformibus, membranaceis, acutis, enerviis. Flores pauci, juveniles soli noti: spatha 3–5 mm. longa, clavata, mucronata, subpapillosa, adulta ignota; tepalis 7, lanceolatis, acutis; staminibus 7, filamentis membranaceis, lanceolatis; antheris obtusis vel emarginatis; granulis pollinis 20 × 11 μ, lobis angustis, ovoideis; ovario ovoideo, acuto, basi rotundato vel attenuato, applanato, costis 8, quarum 2 indistinctis; stylis filiformibus, apice oblique truncatis, facie interne emarginatis. Fructus valvis 2 aequalibus, utraque valva 5-costata, costis prominentibus.

Herb with small shoots arising in pairs from long, thin, flattened roots; base about 0.5 cm. long and wide, 2 mm. thick. Leaves delicate, repeatedly pinnate, 3–6 cm. long, with all the pinnae ascending at an angle of 45–90°; petiole 0.5–1.5 cm. long, about 1 mm. wide, membranaceous, transparent when young, sometimes with a distinct, membranaceous ligule about 1 mm. high at the base; primary pinnae 2.5–15.0 mm. long, pinnate or forked, alternate or slightly opposite; secondary pinnae 2–6 mm. long; tertiary pinnae repeatedly forked, about 2.5 mm. long, the ultimate divisions lanceolate, membranaceous, nearly filiform, acute, nerveless, to 2 mm. long. Flowers few, only young ones known: pedicel 1.5–2.0 cm. long; spathe clavate, mucronate, slightly papillate, 3–5 mm. long; tepals 7, lanceolate, acute, about 0.5 mm. long; stamens about 2.5–3.0 mm. long; filaments membranaceous, lanceolate, 1.5–2.0 mm. long, the anthers obtuse or emarginate, 1.0–1.5 mm. long; pollen 20 × 11 μ, lobes narrow, tapering toward the 2 poles; ovary ovoid, acute, rounded or attenuate at the base, 2.5–3.0 mm. long, about 1.5 mm. wide, flattened, 8-ribbed, all the ribs very slightly raised, 2 of them indistinct; styles 2, filiform with obliquely truncate apex, emarginate at the inner margin, 0.5–1.0 mm. long. Fruit with 2 equal valves, each distinctly 5-ribbed, the ribs slightly raised, 2.5–3.0 mm. long.

CHIRIQUÍ: Boquete, *Woodson & Schery 805* (HOLOTYPE in Gray Herb.; ISOTYPE in Herb. Missouri Bot. Gard.).

This species somewhat resembles young specimens of *Marathrum indifferens* but differs from that species because the rachis and petiole are not winged. It differs from all the other *Marathrum* species in its transparent petioles, its nearly filiform ultimate leaf-divisions which also are transparent, and in the long and very narrow but distinctly 3-sulcate pollen grains. It closely resembles *M. tenue*, but that species has only 2 or 3 stamens and its rachis and petiole are narrowly winged.

5. MARATHRUM **indifferens** v. Royen, sp. nov.

Folia ea *Marathri tenui* simulantia sed basi instructa dilatationem membranaceam distincte punctatam, 3- vel 4-tim pinnata; pinnis primariis ala lata rhachi adnatis, interdum fere oppositis, 60–90° rhachi declinatis; pinnis tertiariis repetito bifurcatis, laciniis ultimis subfiliformibus, acutis, erneviis. Flores pauci; spathellis demum 4–12 mm. longis; pedicello saepe 2-alato; tepalis 5–8, squamiformibus; staminibus 5–8, filamentis lanceolatis, membranaceis, antheris acutis vel emarginatis; granulis pollinis 16 × 14 μ; ovario ovoideo, 8-costato; stylis juvenilibus 0.8 mm., veteribus 1.5–2.0 mm. longis, linearibus, apice emarginato vel acuto.

Small herb; base branched or unbranched, 0.5–4.5 cm. long, 0.5–10.0 mm. high, 1–3 mm. thick. Leaves 0.5–15.0 cm. long, 3–4 times pinnate, with all the pinnae alternate or slightly subopposite and ascending at an angle of 60–90°; primary pinnae 1–3 cm. long, widened in the axil and with a distinct wing decurrent upon the rachis; secondary pinnae 1–4 mm. long, the ultimate divisions 0.5–5.0 mm. long, nearly filiform, acute, nerveless; petiole terete or flattened, widened at

Fig. 59. *Marathrum indifferens*

the base, 0.5–3.5 cm. long, 0.5–1.5 mm. wide, dilated with 2 pointed wings at the base. Flowers few; pedicel terete or sometimes 2-winged, 1.5–5.0 cm. long; young spathe unknown, the older infundibuliform, 4–12 mm. long; tepals 5–8, squamiform, 0.5 mm. long or shorter; stamens 5–8, 3.0–6.5 mm. long, the filaments lanceolate, membranaceous, 2.5–5.0 mm. long, the anthers acute or emarginate, 1.0–2.2 mm. long; pollen ovoid, 16 × 14 μ, 3-lobed, lobes tapering toward one pole; ovary ovoid, acute, base attenuate, 2.2–4.0 mm. long, 1.5–1.8 mm. broad, flattened, 8-ribbed; styles 1–2 mm. long, linear, emarginate or acute. Fruit with 2 equal valves, each 5-ribbed.

Mexico, Guatemala, British Honduras, and Panama.

CANAL ZONE: Río Indio, *Dodge & Allen 17398, 17399* (HOLOTYPE in Herb. Utrecht; ISOTYPE in Herb. Missouri Bot. Gard.); Río Boquerón, *Steyermark & Allen 17256;* Quebrada Ancha, *Steyermark & Allen 17117.* CHIRIQUÍ: San Felix, *Pittier 5430.*

This species closely resembles *M. tenue,* but its rachis and petiole are very distinctly winged; while the latter species has 2–3 stamens, *M. indifferens* has 5–8 stamens. The distinctly pointed dilation at the base of the petioles characterizes *M. indifferens* from all other species of *Marathrum.*

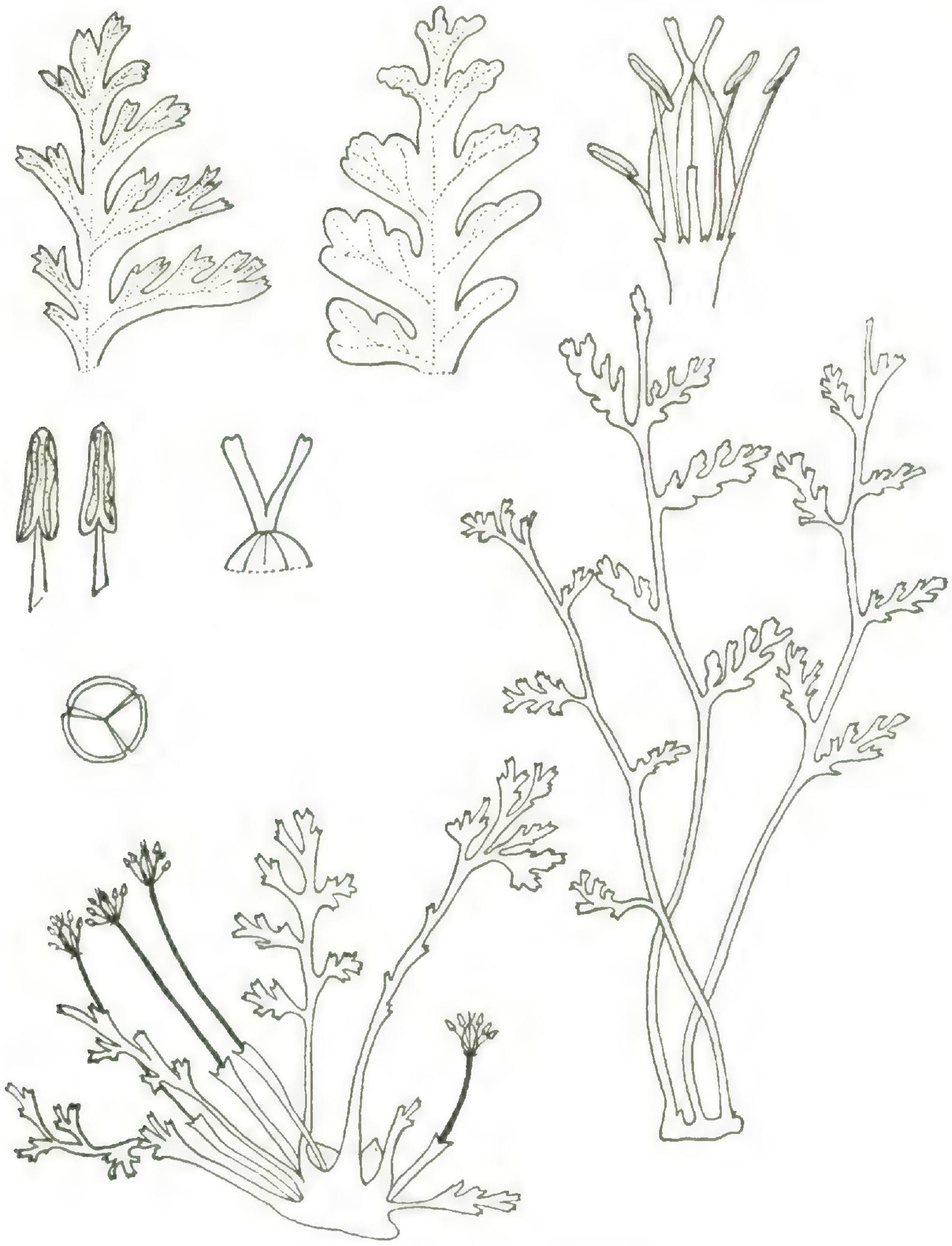

Fig. 60. *Marathrum cheiriferum*

6. MARATHRUM **cheiriferum** v. Royen, sp. nov.

Herba pusilla vel mediocris, acaulis; basi irregulari. Folia bis- vel ter-pinnata, 2–20 cm. longa; pinnis primariis leviter nervatis, 30–45° declinatis, laciniis ultimis ovatis, obtusis vel acutis, leviter nervatis vel enervatis, vel interdum oblongis, rotundatis, margine crenulato-lobatis, 0.3–1.0 mm. longis, 0.3–0.8 mm. latis; petiolo tereti vel applanato, rhachide striata, anguste alata. Flores pauci, solitarii; spathella claviformi, acuta, deinde infundibuliformi; tepalis 6–8, triangularibus, acutis, minus quam 0.5 mm. longis; staminibus 6–8, filamentis subulato-lanceolatis, nervatis, antheris apice obtuso vel mucronato; granulis pollinis globosis, 15 × 14 μ;

ovario ellipsoideo, apice acuto, basi attenuato, costis 8 distinctis, costis suturalibus juventute indistinctis; stylis filiformibus vel spathulatis apice emarginatis, obtusis, basi paullo connatis, leviter papillatis; capsula valvis 2 aequalibus, distincte 8-costatis.

Small to medium-sized herbs; base irregular, 0.5–2.0 cm. long, 2–8 mm. wide, 1–2 mm. thick. Leaves 2–3 times pinnate, with all the pinnae ascending at an angle of 30–45°, 2–20 cm. long; primary pinnae 0.6–4.0 cm. long, 10–20 per leaf, the ultimate pinnae a few times forked; ultimate divisions to 1 mm. long and about 0.5 mm. wide, ovate, obtuse to acute, slightly nerved or nerveless, or the ultimate divisions rotundate and margins crenulate to lobed; petiole terete to flattened, 0.5–5.0 cm. long, 0.5–2.0 mm. wide at the base, the rachis distinctly striate and narrowly winged. Flowers few, solitary; pedicel terete, 0.5–5.0 cm. long; young spathe clavate, acute, 2–5 mm. long, the older infundibuliform, 6–10 mm. long; tepals 6–8, triangular, acute, less than 0.5 mm. long; stamens 6–8, 3.0–5.5 mm. long; filaments at first subulate but later lanceolate, membranaceous, 3-sided at the base, 2.5–4.5 mm. long; anthers obtuse or mucronate, 1.0–1.5 mm. long; pollen globose, slightly 3-sulcate, 17 × 14 μ; ovary ovoid to ellipsoid, acute, base attenuate, slightly flattened, definitely 8-ribbed, 2 of the ribs indistinct, in young flowers 2.5–3.0 mm. long, 1.0–1.5 mm. wide; styles filiform or spathulate, obtuse, emarginate, slightly papillate, 1.0–1.5 mm. long. Fruit with equal valves, each distinctly 5-ribbed.

Costa Rica, Panama, and Colombia.

COCLÉ: Río Mata Ahogada, Valle Chiquita, *Martin 2979;* Río Antón, *Hunter & Allen 351.* PANAMÁ: Río de Jesús, *Bouché s. n.* (HOLOTYPE in Herb. N. Y. Bot. Gard.).

Closely resembles M. *minutiflorum* but is easily distinguished by the shortly triangular ultimate leaf-divisions, those of the latter being spathulate.

7. MARATHRUM ALLENII Woodson, in Ann. Mo. Bot. Gard. 25:827. 1938.

Small herbs; base irregular, sometimes branched, 0.5–7.0 cm. wide, 0.5–4.0 cm. high. Leaves 1–20 cm. long, 3–4 times pinnate, with all the pinnae ascending at an angle of 30–60°; primary pinnae 0.3–3.0 cm. long, membranaceously widened in the axils; secondary pinnae 1–1.5 mm. long, the ultimate pinnae a few times forked, the ultimate divisions spathulate, mostly acute, nerveless or seldom indistinctly nerved, to 1.5 mm. long and 0.3 mm. wide; petiole dilated at the base, with a membranaceous, acute to obtuse or emarginate ligule 1–2 mm. long and 1 mm. wide, which sometimes is markedly shifted toward the ventral side, 0.3–7.0 cm. long, 0.5–2.0 mm. wide. Flowers several; pedicel 1.0–7.5 cm. long, terete or 2-winged; spathe clavate, the young 2–8 mm. long, obtuse or mucronate, smooth or slightly papillate, the older infundibuliform, 7–15 mm. long; tepals 6–9, scale-like, 0.5 mm. long or shorter; stamens 5–9, 4.0–5.5 mm. long, the filaments lanceolate, membranaceous, sometimes split at the top, the anthers acute, obtuse or emarginate,

Fig. 61. *Marathrum Allenii*

1.0–2.5 mm. long; pollen ellipsoidal, 17 × 14 μ, the lobes tapering toward one pole; ovary ovoid or ellipsoid, 3.5–4.0 mm. long, terete, acute, sessile or attenuate at the base, 8-ribbed, the ribs slightly raised; styles filiform, narrow, 3-sided at the base, obtuse or slightly emarginate, papillate, nerved, 0.5–2.0 mm. long. Fruit with 2 equal 5-ribbed valves, the ribs but slightly raised.

Panama.

CHIRIQUÍ: Remedios, *Pittier 5443*. COCLÉ: El Valle de Antón, *Allen 82*; same locality, *Woodson & Schery 160*.

8. MARATHRUM FOENICULACEUM Humb. & Bonpl. Pl. Aequinox. 1:40, *tab. II.* 1808.

Lacis foeniculacea (H. & B.) Mart. Nov. Gen. & Sp. 1:6. 1824.

Medium-sized herb; base irregular, 0.5–2.0 cm. long, 1.0–1.5 cm. wide. Leaves 2.5–35.0 cm. long, repeatedly bifurcated or rarely 3–6 times pinnate; lateral lobes 3–6 times bifurcated or rarely pinnate, 0.5–10.0 cm. long, ascending at an angle of 30–60°, the ultimate divisions 0.5–12.0 mm. long, narrow, obtuse or acute, nerveless or very rarely nerved; petiole 1–8 cm. long, flattened, membranaceously widened at the base, with a distinct, sometimes very irregular ligule 2–3 mm. long and 5 mm. wide. Flowers solitary or in fascicles between the leaf bases; pedicel 1.0–1.5 cm. long, thickened into a disc at the tip; young spathe acute, 0.5–1.0 cm. long, the older tubular or infundibuliform, 0.5–1.0 cm. long; tepals 5–8, triangular, acute or acuminate, about 1 mm. long; stamens 5–8, 3.5–5.5 mm. long, the filament lanceolate, scaphiform at the base, sometimes slightly united, 3–4 mm. long, the anthers obtuse, about 1 mm. long; pollen nearly globose, about 18 × 15 μ, the lobes very wide at one pole and tapering toward the other; ovary ellipsoid, acute, base attenuate, flattened, distinctly 8-ribbed, 3.0–4.5 mm. long, 1.0–1.5 mm. wide; styles flattened or subulate, acute or emarginate, 1.0–2.5 mm. long. Fruit dehiscing with 2 equal, 5-ribbed valves.

Mexico to Colombia.

PANAMA: locality unknown, *Hayes 824.*

SAXIFRAGACEAE

BY ELIZABETH McCLINTOCK

Deciduous or evergreen shrubs or small trees, or perennial, rarely annual, herbs. Leaves alternate or opposite, mostly simple but variable in form, usually without stipules. Inflorescence various; flowers mostly perfect and actinomorphic, medium-sized or small, rarely large and showy; receptacle various, flat or often concave and forming a hypanthium more or less adnate to the ovary; sepals 4 or 5, rarely more; petals as many as the sepals, imbricate or valvate, free; stamens as many as petals and alternate with them, or twice as many as petals, rarely more numerous; filaments subulate or filiform; anthers rotund or oblong, 2-celled, opening lengthwise; carpels usually united and fewer than petals, seldom partially free and equal in number to the petals; ovary superior or partly or wholly inferior, placentae parietal or axillary, rarely otherwise, ovules usually numerous, styles the same number as carpels, free or partially united. Fruit a dehiscent capsule or a berry; seeds usually numerous, small and occasionally winged.

About 70 genera, widely distributed in both hemispheres, mostly in temperate to subarctic regions, rare in the tropics where only certain woody genera are found. Four genera in Panama.

The Central and South American species of *Hydrangea* belong to the Section Cornidia Engler (Nat. Pflanzenfam. 3^{2a}:76. 1890), characterized by being evergreen climbers or shrubs with coriaceous leaves. Cornidia does not occur exclusively in the New World, several species having been described from the Philippine Islands and Formosa. In addition to Cornidia there are two other sections in the genus which occur in the eastern United States and in China and Japan where the genus is concentrated.

There are two types of inflorescence in Cornidia. The most common consists of a single cyme, with or without sterile flowers. The second type consists of several cymes one above the other, and does not have sterile flowers. The Central American species have only the first type, but both types are found in the South American species. The characters distinguishing the species within each group are usually found in the flowers: in the presence or absence of sterile flowers, in the size, shape and number of styles, and in the length of the stamens. Because of the small size of the flowers these differences are not readily seen.

Sterile, juvenile plants, quite different from the adult flowering plants, have been collected in Central and South America in areas where the genus occurs. Juvenile plants have small, membranous, serrate or entire leaves borne on slender climbing stems. There are no distinctive generic or specific characters associated with these plants, and they passed unrecognized until they were finally associated with *Hydrangea*.

a. Flowers epiphyllous, borne in few-flowered cymes along the midvein on the upper leaf surface, inconspicuous, greenish; petals less than 1 mm. long; fruit a few-seeded berry ..... 4. Phyllonoma
aa. Flowers not epiphyllous, conspicuous, white or colored; petals 2 mm. or more long; fruit a many-seeded capsule.
  b. Inflorescence a many-flowered cyme, often bearing a few large sterile flowers in addition to the smaller, fertile ones; fertile flowers with petals about 2 mm. long, deciduous during anthesis; stamens twice as many as petals; capsule opening at apex between the styles; styles developing during maturity of fruit to about double their size in anthesis ..... 1. Hydrangea
  bb. Inflorescence a few-flowered cyme, or flowers borne singly, flowers alike; petals 10 mm. or more long, persistent during anthesis; stamens same number as petals or numerous; capsule opening from base between the valves or from the apex loculicidally; styles not developing further during maturity of fruit.
    c. Sepals and petals 4, stamens numerous; petals 15–20 mm. long, obovate, spreading; capsule dehiscent loculicidally from apex; leaves deciduous; leaves and branchlets hirsute-strigose ..... 3. Philadelphus
    cc. Sepals, petals and stamens 5; petals 10 mm. long, linear-spathulate, erect, appearing to cohere and to form a tubular corolla; capsule dehiscing from base between the valves; leaves evergreen; leaves and branchlets resinous and glandular ..... 2. Escallonia

1. HYDRANGEA L.

Hydrangea L. Sp. Pl. 397. 1753.

Cornidia Ruiz & Pav. Fl. Peruv. et Chil. Prodr. 53, *t. 35*. 1794.
Sarcostyles Presl, ex DC. Prodr. 4:15. 1830.

Woody climbers or shrubs, inflorescence and adjacent stem pubescent with stellate hairs, or tomentose with long, curling silky hairs. Leaves opposite, simple, blades penninerved, margins remotely denticulate or entire, oval, broadest near middle, petiole stout. Inflorescence cymose (in Central America), terminal, or occasionally lateral, subtended by chartaceous, caducous involucral bracts; sterile flowers showy, pink or white, not always present; fertile flowers white or maroon, small; hypanthium hemispheric; calyx-lobes 4, inconspicuous, deltoid; petals 4, oblong, valvate, deciduous during anthesis; stamens 8, occasionally 10, filaments long and filiform or short and inconspicuous, anthers oblong to somewhat rounded; ovary inferior, 2- to 4-celled, styles 2–4, erect and spreading, or occasionally coherent in bud and early anthesis, continuing to elongate with the maturing capsule; stigmas terminal and more or less decurrent on inner surface; ovules numerous, borne on axial placentae; capsule 2- to 4-celled, truncate, thick-walled, dehiscent at apex between the spreading styles; seeds numerous, very small, linear, arcuate.

a. Sterile flowers present; styles usually 2, slender or clavate.
  b. Stamens conspicuous, filaments 1–3.5 mm. long, 2–7 times as long as styles; styles (during anthesis) less than 1 mm. long, slender, acute at apex ..... 1. H. Oerstedii
  bb. Stamens inconspicuous, filaments 0.2–0.9 mm. long, shorter than styles; styles (during anthesis) 1–2 mm. long ..... 2. H. peruviana
aa. Sterile flowers absent; styles usually 3, thickened at base ..... 3. H. Preslii

1. Hydrangea Oerstedii Briq. in Ann. Conserv. & Jard. Bot. Genève 20:407. 1919.

Cornidia radiata Oerst. in Naturhist. Foren. Kjoeb. Vidensk. Meddel. 42. 1856, non *Hydrangea radiata* Walt. Fl. Carol. 251. 1788.
Hydrangea durifolia Briq. loc. cit. 406. 1919.
Hydrangea Goudotii Briq. loc. cit. 404. 1919.
Hydrangea platyphylla Briq. loc. cit. 401. 1919.
?*Hydrangea Seemannii* Riley, in Kew Bull. Misc. Inf. 207. 1924.

Woody climbers or shrubs, pubescence of stellate hairs, sparse to moderate on inflorescence and adjoining stem, occasionally densely pubescent with long curling hairs *(Woodson & Schery 511)*; leaves oval, 10–15 cm. long, 4–7 cm. wide, their length 2 to 2½ times their width (Central America), usually pubescent as the inflorescence on lower surface, upper surface glabrous, margin remotely denticulate to nearly entire, petiole stout, 1–2 cm. long; inflorescence open and spreading, longest branches 4–10 cm. long; sterile flowers present, pink, fertile flowers maroon; hypanthium 1–1.5 mm. long; calyx-lobes 0.5 mm. long; petals 1–2 mm. long, 1 mm. wide; stamens 8, 2–4.5 mm. long, filaments 1–3.5 mm. long, 2 to 7 times as long as styles; styles 2, rarely 3, 0.3–1 mm. long (during anthesis), slender, acute at apex, stigma inconspicuous; capsule 2 mm. long, 2.5 mm. wide at apex, mature styles 2 mm. long.

? Mexico, Costa Rica to Peru.

CHIRIQUÍ: central valley of Río Chiriquí Viejo, 1800–2000 m., *Allen 1400;* Bajo Mono and Quebrada Chiquero, 1500 m., *Woodson & Schery 511.* COCLÉ: region north of El Valle de Antón, 1000 m., *Allen 2693, 3712.*

2. Hydrangea peruviana Moric. in DC. Prodr. 4:14. 1830.

Cornidia peruviana (Moric.) Small, in N. Am. Fl. 22:161. 1905.
Hydrangea Trianae Briq. in Ann. Conserv. & Jard. Bot. Genève 20:403. 1919.
Hydrangea panamensis Standl. in Jour. Wash. Acad. Sci. 17:10. 1927.
Hydrangea Weberbaueri Engler, in Engl. & Prantl, Nat. Pflanzenfam. 18a:207. 1930.
Hydrangea caucana Engl. loc. cit. 206. 1930.

Woody climbers or shrubs, pubescence of stellate hairs, sparse to moderate on inflorescence and adjoining stem; leaves oval, 10–23 cm. long, 5–14 cm. wide, their length 2 to 3 times their width, both surfaces usually glabrous, margin entire to remotely denticulate; inflorescence open and spreading, longest branches 5–15 cm. long; sterile flowers present, pink, fertile flowers maroon, hypanthium 1.5 mm. long; calyx-lobes 0.4 mm. long; petals 1.5 mm. long, 1 mm. wide; stamens 8, 0.4–1.6 mm. long, filaments 0.2–0.9 mm. long, always shorter than styles; styles 2, rarely 3, 1–2 mm. long (during anthesis), clavate, stigma conspicuous, extending from apex along inner surface; capsule 2 mm. long, 2.5 wide at apex, mature styles 2 mm. long.

Costa Rica to Peru.

Colón: along Río Fato, 10–100 m., *Pittier 3010*. Chiriquí: Boquete Distr., Bajo Chorro, 2000 m., *Davidson 74*; valley of the upper Río Chiriquí Viejo, *White 90a*.

Hydrangea peruviana Moric. is very close to *H. Oerstedii* Briq. They are similar in habit, vegetative characters and fruits, and both have showy, pink, sterile flowers. Their only difference lies in the length of their stamens and styles. In *H. Oerstedii* the filaments are several times longer than the styles. The styles are slender, lack a prominent stigmatic surface and are less than 1 mm. in length. The prominent stamens can be seen with a lens or even the naked eye. The filaments of *H. peruviana*, on the other hand, are shorter than the styles which are clavate and from 1 to 2 mm. long. With the aid of a hand-lens it should be possible to distinguish between these two species in the field, provided that flowers are present.

3. Hydrangea Preslii Briq. in Ann. Conserv. & Jard. Bot. Genève 20:409. 1919.

Cornidia umbellata Ruiz & Pav. Syst. Veg. 91. 1798.
Sarcostyles peruviana Presl, ex DC. Prodr. 4:15. 1830, non *Hydrangea peruviana* Moric. in DC. Prodr. 4:14. 1830.
Hydrangea umbellata Briq. loc. cit. 411. 1919, non Rehder.
Hydrangea ecuadorensis Briq. loc. cit. 410. 1919.
Hydrangea Briquetii Engler, in Engl. & Prantl, Nat. Pflanzenfam. 18a:207. 1930.

Woody climbers or shrubs, pubescence of stellate hairs sparse to moderate on inflorescence and adjoining stem; leaves oval, 9–20 cm. long, 4–9 cm. wide, their length 2 to 3 times their width, margin entire and somewhat undulate, petiole stout, 15–20 mm. long; inflorescence more or less compact, longest branches 4–9 cm. long, sterile flowers absent, fertile flowers maroon; hypanthium 1.5 mm. long; calyx-lobes 0.5 mm. long; petals 1.5–2 mm. long, 1 mm. wide; stamens 8, 1.5–2 mm. long, filaments 1–1.5 mm. long, approximately as long as styles (in Central America); styles usually 3, occasionally 2 or 4, 0.8–1.5 mm. long (during anthesis),

Fig. 62. *Hydrangea peruviana*

thickened at base, stigma usually extending from apex along inner surface; capsule 2 mm. long, 2.5 mm. wide at apex, mature styles 1.5–2 mm. long.

Costa Rica, Panama, Ecuador, and Peru.

COCLÉ: vicinity La Mesa, hills north of El Valle de Antón, 1000 m., *Allen 2332*.

Hydrangea Preslii differs from the other two species in the lack of sterile flowers and in the number and shape of the styles. The styles are usually 3, although occasional flowers may have 2 or 4. They are thickened at the base and attenuate toward the apex, while in the others they are slender or clavate.

2. ESCALLONIA Mutis

ESCALLONIA Mutis ex L. f. Suppl. 21. 1781.

Stereoxylon Ruiz & Pav. Fl. Peruv. et Chil. Prodr. 38, *t. 6*. 1794.

Small trees or shrubs, evergreen, rarely deciduous. Leaves alternate, shortly petiolate, lanceolate, oblong-elliptic or lance-obovate, mostly leathery and glandular-serrate. Inflorescence racemose or paniculate, few- to many-flowered, or flowers borne singly; hypanthium nearly globose or turbinate, completely or partially united to ovary, calyx-lobes 5, ovate, subulate at apex; petals 5, imbricate in bud, linear-spathulate, with long, erect claws which appear to be coherent and to form a tubular corolla, bearing at their apices spreading blades; stamens 5, inserted on margin of hypanthium, erect; filaments filiform, anthers oblong-ovoid; ovary with 2–3 complete or incomplete chambers, with 4–6 placentae which hang from an apical, central axis and bear numerous ovules; style mostly simple, rarely 2-parted at apex, with capitate or lobed stigma; capsule with 2–3 chambers, septicidally dehiscent from the base into 2 or 3 valves which hang together by the bundles of the hypanthium and the partitions, after the partial or complete shedding of the epicarp (hypanthial wall and style); seeds many, usually small, often curved, with longitudinal grooves in the covering, fimbriate at base.

A large genus, mostly of the Andes and southern Brazil in South America, with two species in the mountains of Central America. One species in Panama.

1. ESCALLONIA POASANA Donn. Sm. in Bot. Gaz. 23:243–244. 1897.

Small tree up to 25 feet tall, irregular in shape; branchlets short, closely leafy, somewhat resinous and glandular; leaves 10–20 mm. long, 6–9 mm. wide, obovate, rounded at apex, cuneate at base and narrowed to a short petiole 2–3 mm. long, margins finely denticulate, at least in upper half, somewhat resinous, subcoriaceous, lower surface whitened and reticulate, upper surface green; flowers white, borne singly, apically or laterally, on the short branchlets, peduncles 5–15 mm. long; hypanthium united to ovary in lower half, 7 mm. long, diameter at upper margin 6 mm., calyx-lobes 2 mm. long, deltoid, acuminate toward apex, margins fimbriate; petals 10 mm. long, blade 3 mm. long, scarcely broader than claw, rounded at apex with a short mucro at tip, margins fimbriate; stamens 7.5 mm. long, filaments 5

mm. long, anthers oblong; style entire, 5 mm. long, stigma depressed-globose, crenate on margin; capsule 7–8 mm. long, at upper margin 7 mm. in diameter, bilocular, dehiscent at base.

Costa Rica and Panama.

CHIRIQUÍ: Boquete Distr., Volcán de Chiriquí, 10,400 ft., *Davidson 1054, 1306;* Chiriquí Volcano, 2800–3000 m., *Pittier 3079;* Río Chiriquí Viejo, *White 6.*

3. PHILADELPHUS L.

PHILADELPHUS L. Sp. Pl. 470. 1753.

Syringa Adans., Fam. Pl. 2:244. 1763.

Deciduous shrubs with slender, arching and occasionally scandent stems with close or sometimes flaking bark. Leaves opposite, entire or dentate, sessile or shortly petiolate, lower surface often pubescent with simple hairs, upper surface green and glabrous or with few scattered pili, usually with 3–5 prominent veins from base. Flowers white, showy, often fragrant, solitary or in few-flowered terminal cymes; hypanthium turbinate, united with the ovary, calyx-lobes 4, rarely 5–6; petals 4, rarely 5–6, obovate, rounded or retuse at apex, convolute in bud; stamens 20 or more, filaments flat, subulate, anthers small, oblong; ovary inferior to half superior, 4 or rarely 3 or 5 chambers, placentae axial, bearing numerous ovules; styles 3–5, filiform, more or less united, each bearing an elongate stigma; capsule turbinate, ligneous or coriaceous, 3–5 chambers, dehiscing loculicidally from the top; seeds numerous, oblong.

About 40 species in North and Central America, eastern Asia and southern Europe.

1. PHILADELPHUS MYRTOIDES Bertol. Fl. Guat. 21, *tab. 7* (in Nov. Comm. Acad. Sci. Inst. Bonon. 4:421, *pl. 43*). 1840.

Philadelphus trichopetalus Koern. in Regel's Gartenfl. 16:73. 1867.

Shrub with arching, strigose and often scandent stems; leaves 3–9 cm. long, ovate, acuminate at apex, rounded at base, remotely denticulate, 3- to 5-nerved at base, pale and hirsute-strigose beneath, green with few pili above, short-petiolate; flowers pedicellate, 1–3, on short branchlets; hypanthium and calyx grayish-strigose, calyx-lobes 5–10 mm. long, deltoid-acuminate; petals 15–20 mm. long, broadly obovate or suborbicular, glabrous or finely villous on both surfaces; stamens and style about one-half as long as petals; capsule 10 mm. long.

Guatemala, also in Costa Rica and Panama, but perhaps indigenous only in Guatemala. Close to *Philadelphus mexicanus* Schlecht. of southern Mexico.

CHIRIQUÍ: Bajo Mona and Quebrada Chiquero, 1500 m., *Woodson & Schery 588*—"Side of a footpath, possibly an escape."

4. PHYLLONOMA Willd.

Phyllonoma Willd. ex Roem. and Schult. Syst. Veg. 6:210. 1820.

Dulongia HBK. Nov. Gen. & Sp. 7:76. 1825.

Shrubs or small trees, completely glabrous; leaves alternate, membranous or coriaceous, lanceolate to ovate-lanceolate, long-acuminate toward apex, entire or denticulate, petiolate. Inflorescence few- to many-flowered, cymose or racemose, arising from the midvein on the upper surface of the leaves near the base of the acuminate tip; flowers small, greenish-white; hypanthium turbinate, completely attached to ovary, disc epigynous, thick, covering base of petals and stamens; calyx-lobes 5, deltoid, minute; petals 5, valvate in bud, spreading in anthesis, deltoid-ovate, acute at apex; stamens 5, alternating with petals, spreading, filaments short, subulate; ovary inferior, 1-celled with 2 rows of erect ovules on 2 parietal placentae, very short, styles 2, scarcely protruding from disc, spreading, with stigmatic surface at apex; fruit a berry, with scars of sepals and petals at apex, imperfectly 2-celled; seeds 3–6, small, oblong.

Fig. 63. *Phyllonoma ruscifolia*

A small genus occurring from the high mountains of southern Mexico through the Andes to Bolivia, with one species in Panama.

1. Phyllonoma ruscifolia Willd. ex Roem. and Schult. Syst. Veg. 6:210. 1820.

Dulongia acuminata HBK. Nov. Gen. & Sp. 7:78, *pl. 623*. 1825.

Small tree to 20 feet; leaves ovate-lanceolate, coriaceous, blade 40–85 mm. long, 10–30 mm. wide, gradually narrowed to the slender pointed acumen 10–25 mm.

long, remotely denticulate below acumen nearly to base; inflorescence immediately below acumen or on its lower half, several-flowered; hypanthium broadly turbinate, disc 0.7 mm. across; calyx-lobes 0.2 mm. long; petals 0.5 mm. long; stamens less than half as long as petals; styles and stigmas 0.1 mm. long; berry 4 mm. in diameter, white turning black on drying.

Costa Rica to Bolivia.

CHIRIQUÍ: Boquete Distr., Cerro Horqueta, *von Hagen 2043*.

CUNONIACEAE

1. WEINMANNIA L.

WIENMANNIA L. Syst. ed. 10, 2:1005. 1759; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 18a:250. 1930.

Arnoldia Bl. Bijdr. 868. 1826.
Leiospermum D. Don, in Edinb. New Phil. Jour. 9:91. 1830.
Pterophylla D. Don, loc. cit. 93. 1830.
Ornithropus Boj. ex Engl. in Linnaea 36:636. 1870.

Trees or shrubs, the younger branches usually somewhat flattened and rotating to about 45° between the nodes. Leaves opposite, usually imparipinnate, often with the rachis winged between the opposite leaflets, rarely simple; stipules interpetiolar, caducous. Inflorescence frequently appearing terminal but axillary and usually opposite in the upper leaf-axils, a racemiform or spiciform thyrse with the pedicels clustered and nearly sessile upon the short side branches. Flowers numerous, small, perfect or polygamo-dioecious; sepals 4–5; petals 4–5, white or somewhat pinkish; stamens 8–10; ovary superior, 2- or rarely 3-celled, each carpel with a gradually produced, persistent style with simple stigma; ovules numerous, in 2 rows upon the axile placentae; disc fleshy, hypogynous, surrounding the ovary but free from the stamens. Fruit a small, thin, septicidally 2- or rarely 3-valved capsule; seeds small, usually pilose.

Weinmannia is a genus of upward of 100 species of the tropics and subtropics of both hemispheres. The species are notoriously variable, and much confusion has resulted from the failure of certain students to appreciate this fact.

a. Leaves imparipinnate, the rachis broadly winged between the small leaflets; flowering branches relatively distant, the inflorescences not greatly aggregated ..... 1. W. PINNATA
aa. Leaves simple; flowering branches conspicuously shortened, the inflorescences appearing greatly aggregated ..... 2. W. PSEUDOLAURINA

1. WEINMANNIA PINNATA L. Syst. ed. 10, 2:1005. 1759.

Weinmannia glabra L. f. Suppl. 228. 1781 (based on *W. pinnata* L.).
Weinmannia intermedia Cham. & Schlecht. in Linnaea 5:555. 1830.
Weinmannia burseraefolia Standl. in Jour. Wash. Acad. Sci. 17:310. 1927.
Weinmannia Liebmannii Engl. in Engl. & Prantl, Nat. Pflanzenfam. 18a:252. 1930, nom. subnud.

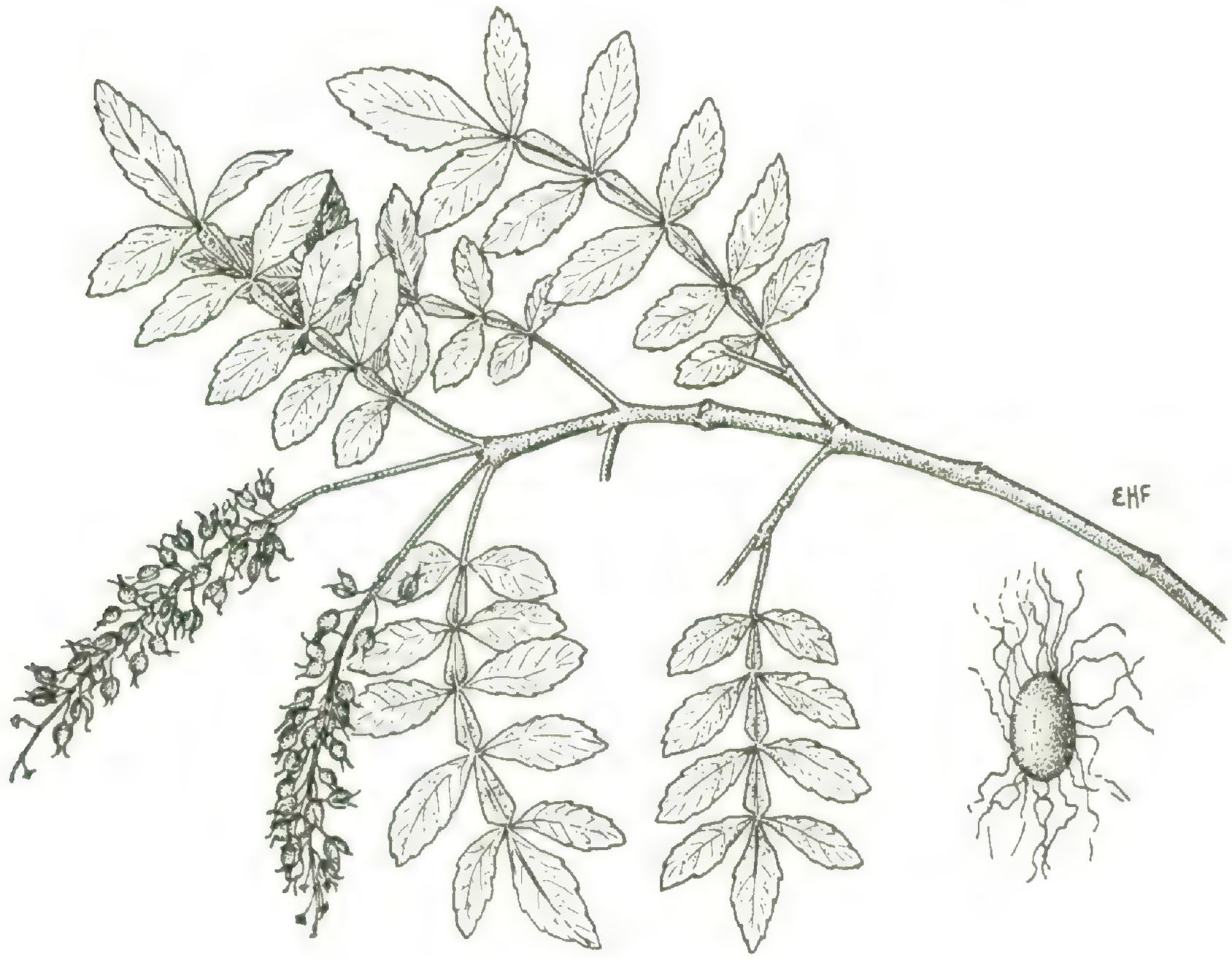

Fig. 64. *Weinmannia pinnata*

Large shrub or small tree sometimes as much as 20 m. tall, the younger branches ferruginous-pilose to glabrate. Leaves imparipinnate, petiolate, 3–9 cm. long, the rachis broadly winged in rhombic sectors between the pairs of leaflets; lateral leaflets in 2–6 pairs, oblong-elliptic to obovate, unequally cuneate at the base, acute or obtuse at the tip, rather closely crenulate, about 0.7–3.0 cm. long and 0.5–1.0 cm. wide, wholly glabrous or more or less pubescent beneath; terminal leaflet usually somewhat larger and more symmetrical than the lateral, rhombic-elliptic to obovate, obtuse to acuminate; petiole 0.7–2.0 cm. long. Inflorescences usually distinctly paired in the axils of the uppermost pair of leaves, narrowly cylindrical, 2–9 cm. long, the pedicels 2–3 mm. long, slender, usually more or less ferruginous-pilose like the peduncle; sepals triangular, persistent in fruit, about 1 mm. long; petals white or rarely pinkish, slightly longer than the sepals; stamens with white filaments 2–3 mm. long, the small anthers orange. Capsule glabrous, 3–4 mm. long; seeds pilose.

Southern Mexico to Brazil and Peru; Cuba, Jamaica, and throughout the Antilles, growing in forests as a rule, at temperate altitudes.

CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, alt. 1300–1900 m., *Seibert 288;* summit of Cerro Copete, alt. 9000 ft., *Allen 4892;* Finca Lérida to Peña Blanca, *Woodson & Schery 330;* Volcán de Chiriquí, *Davidson 977;* Cerro Horqueta, cloud forest, alt. 6500 ft., *von Hagen & von Hagen 2068;* vicinity of Finca Lérida, upper forested slopes of Quebrada Velo, alt. 5000 ft., *Allen 4736;* vicinity of Casita Alta, Volcán de Chiriquí, *Woodson, Allen & Seibert 821.*

Weinmannia pinnata is a very frequent tree in Chiriquí at altitudes between approximately 1200 and 2500 m. The number, size, and shape of the leaflets, as well as their indument, is exceedingly variable; this has given rise to a formidable array of "species", only the more important of which, from Central America alone, are enumerated above. It is very difficult to understand why Engler (loc. cit. 1930) chose the name *W. glabra* L. f. for the nucleus of this complex, when that name is so clearly based upon the earlier *W. pinnata* L.

2. WEINMANNIA PSEUDOLAURINA Woodson, Ann. Mo. Bot. Gard. 28:429. 1941.

Trees at least 8 m. tall; branches strongly compressed and densely ferruginous-pilosulose when young, the flowering internodes greatly contracted. Leaves simple, shortly petiolate, broadly elliptic or elliptic-ovate, rather distantly crenulate, apex obtuse or broadly acute, base obtuse or broadly rounded, 5–9 cm. long, 3.5–5.0 cm. broad, subcoriaceous, glabrous above, inconspicuously pilosulose to glabrate beneath; petiole 2–5 mm. long. Inflorescences densely aggregated in pairs at the tips of the shortened flowering internodes, racemiform, narrowly cylindrical, 6–8 cm. long, the pedicels 3–4 mm. long, ferruginous-pilosulose like the peduncle; sepals persistent in fruit, triangular, about 1 mm. long, very minutely pilosulose; petals unknown; stamens 10, the filaments glabrous, about 2 mm. long. Capsules ovoid, about 3 mm. long, densely ferruginous-pilosulose; seeds densely plumose at both ends.

Endemic tree "very common along edges of grasslands" at altitudes of 600–800 m.

PANAMÁ: Cerro Campana, trail from Campana to Chica, *Allen 2656*.

This species is particularly conspicuous, and unique amongst Weinmannias of its immediate alliance, because of the densely aggregated inflorescences.

ROSACEAE

BY ROGERS McVAUGH

Herbs, shrubs or trees with leaves alternate, rarely opposite, simple or compound, usually with conspicuous stipules. Flowers usually perfect and regular, the perianth perigynous, the axis sometimes enlarged to form a flat or concave receptacle or hypanthium bearing the calyx-lobes, petals, and stamens on its margin, and usually lined inside with a glandular disk; calyx-lobes 5 (sometimes 4), imbricate; petals usually 5 and imbricate, sometimes wanting; stamens few to many, often about 20; carpels 1 to many, distinct or united, often connate with the receptacle; styles as many as the carpels, sometimes connate. Fruit various; seeds usually without appreciable endosperm, the cotyledons often fleshy and convex, rarely folded or convolute.

The Rosaceae comprise approximately 100 genera, well represented in almost all parts of the world. They include many plants of economic importance, especially in temperate regions where they are much cultivated for food and orna-

ment (e. g., the genera *Fragaria, Rubus, Rosa, Spiraea, Prunus, Pyrus, Malus, Chaenomeles, Rhodotypus*, etc.). Some workers have advocated the division of the family into several segregate families, on the basis of characters of the fruit; thus genera with the fruit an achene or a follicle have been made to constitute the Rosaceae proper, genera with drupaceous fruit the Amygdalaceae, and genera with pomaceous fruit the Malaceae. These segregations appear unjustified because of the very large number of characters of the flowers, inflorescences and vegetative parts which are repeated in genus after genus without regard to fruit type, and which together make of the inclusive Rosaceae an easily comprehensible and evidently natural group of related genera. Precise determination of specific limits is difficult in many genera, related groups often seeming to merge morphologically or to differ by minor characters only. Apparently much of the difficulty arises from the frequent occurrence in the family of reproductive methods other than a sexual fusion of haploid gametes followed by regular reduction-division. Several genera are known to include species in which polyploidy, aneuploidy, apomixis and other irregularities have been demonstrated, and it may be supposed that these phenomena have contributed largely to the formation of the numerous minor geographic races which are known to exist, in nature isolated in small disjunct areas or if growing with other related species then barely distinguishable from them.

a. Leaves pinnately or palmately compound, with 3 or more leaflets.
  b. Upright or trailing shrubs with prickly canes and leaves (brambles); petals present and conspicuous; fruit of few or numerous drupelets borne on an enlarged receptacle ..... 3. Rubus
  bb. Herbaceous or low suffrutescent plants with unarmed leaves and stems; corolla wanting.
    c. Hypanthium covered with barbed spines, in fruit forming a bur; erect plants up to 1 m. tall, the inflorescence spicate or racemose .... 5. Acaena
    cc. Hypanthium unarmed; flowers very small (rarely as much as 3 mm. long); plants mostly prostrate or procumbent, the inflorescence cymose, often corymbiform ..... 4. Alchemilla
aa. Leaves simple.
  b. Herbaceous, usually prostrate plants with lobed leaves; flowers very small (rarely as much as 3 mm. long); corolla wanting; calyx-lobes alternating with bracts, the lobes apparently 8–10 in number; hypanthium at maturity containing a few achenes ..... 4. Alchemilla
  bb. Shrubs or trees with simple unlobed leaves; flowers larger; corolla usually present; calyx-lobes usually 5, without alternating bractlets; fruit dry or fleshy.
    c. Styles 5, distinct; fruit of 5 thin-walled achenes, or of 5 bony nutlets in a fleshy hypanthium (pome); leaves dentate.
      d. Fruit of 5 achenes about 2 mm. long; unarmed shrubs with leaves white-tomentose beneath, and flowers in ample panicles 5–15 cm. long ..... 1. Holodiscus
      dd. Fruit a pome up to 1 cm. long, red or black; spinescent shrubs, nearly glabrous or the branchlets rufous-pubescent, the flowers in corymbose cymes 2–3 cm. long ..... 2. Hesperomeles
    cc. Style 1; fruit a dry or fleshy drupe with a single large stone; leaves entire.
      d. Style terminal on the ovary or essentially so; stamens usually 20; flowers (in Panamanian species) in glabrous simple axillary racemes which are ebracteate at flowering time ..... 6. Prunus

dd. Style arising from the base of the ovary; stamens usually 15 or fewer; flowers in cymes or panicles, if in simple racemes these bracteate and pubescent.
e. Filaments 10–16 mm. long; stamens 3–7 ..... 9. HIRTELLA
ee. Filaments 1–6 mm. long; stamens 15–20 (–30?) or if only about 3 anther-bearing, then less than 1 mm. long.
f. Hypanthium 5–6 mm. long (excluding the calyx-lobes) in bud, elongate, somewhat gibbous, the ovary attached laterally somewhat above the base of the hypanthium-cavity ..... 10. COUEPIA
ff. Hypanthium 3 mm. long or less in bud and in anthesis, cup-shaped or campanulate, symmetrical, the ovary attached at the base of the internal cavity.
g. Flowers 8–20, in nearly sessile axillary cymes (2–4 cm. long) shorter than the leaves; low shrub, or medium-sized tree up to 5–6 m. tall ..... 7. CHRYSOBALANUS
gg. Flowers very numerous, in axillary and terminal panicles 10–40 cm. long, with divaricate leafless branches; trees, often 10–15 m. tall or more ..... 8. LICANIA

A weedy immigrant from the United States, *Potentilla norvegica* L., was reported from San José Island by Johnston (Sargentia 8:31, 132. 1949). It is not to be expected that this species will maintain itself permanently in competition with the native flora. It is a hirsute herbaceous annual or biennial with 3-foliolate leaves, leafy cymes, and conspicuous yellow flowers.

1. HOLODISCUS (Koch) Maxim.

HOLODISCUS (Koch) Maxim. in Acta Hort. Petrop. 6:253. 1879; Focke in Engl. & Prantl, Nat. Pflanzenfam. 3^3:18. 1894; Ley in Bull. Torrey Bot. Club 70:275–288. 1943, nom. conserv.

Sericotheca Raf. Sylva Tellur. 152. 1838; Rydb. in N. Am. Fl. 22:261–266. 1908.
Spiraea sect. *Holodiscus* Koch, Dendr. 1:309. 1869.

Deciduous shrubs or small trees up to 7 m. tall, with simple, short-petiolate, estipulate, dentate leaves, the blades mostly with a long cuneate entire base, the veins ascending and parallel to the cuneate base, impressed on the upper surface, the lower surface often tomentose. Flowers white, 5-merous, in large terminal panicle-like clusters; pistils distinct, 2-ovulate, alternate with the sepals, inserted on center of disk, each forming at maturity an indehiscent 1-seeded dry fruit.

This genus has experienced several systematic revisions, and those who have worked on it have usually recognized two principal species-groups, one ranging from British Columbia to northern Mexico, the other from southern Mexico to Colombia. The southern group has been distinguished by having long-mucronate teeth on the leaf-blades, by having the stamens not longer than the sepals, and by the rather strongly pubescent outer surface of the petals. The two most recent monographers of *Holodiscus*, Rydberg (in the North American Flora) and Ley (in the Bulletin of the Torrey Botanical Club) each recognized three species in this "southern group" of the genus, although the two authors differed in their ideas of how the species were to be delimited.

Examination of large series of specimens from western United States indicates that neither author is conservative in delimitation of species, each upholding as species several groups which are morphologically scarcely distinguishable, and in addition are connected by numerous intermediates. The differences between the supposed species are chiefly those in the leaves, which vary in size, shape and vestiture. Study of the meager amount of Central American and South American material which is available indicates that all the supposed species of the above "southern group" are in actuality but representatives of a single species. The leaves are usually oblanceolate or obovate, with the lower surface tomentose and bearing in addition few or many straight silky hairs. Rydberg and Ley have attempted to separate species here on the basis of the pubescence of the upper and lower surfaces of the leaves, respectively, and Ley has also used the shape of the leaf-tip as a criterion. These characters do not seem to be correlated with other morphological ones, however, nor with any geographical area, and in any case both characters are notably untrustworthy in the Rosaceae. The single Panamanian specimen which has been available for study has some leaves rounded at tips and others acute (the usual condition in this genus and other rosaceous ones, the rounded ones being produced first at the initiation of the growing season), so that according to Ley's key it could be either *Holodiscus argenteus* or *H. fissus;* many of the leaves agree precisely in shape with her illustration (Bull. Torrey Bot. Club 70:287, *fig. 3.* 1943) of *H. argenteus,* but the pubescence of the lower surface is less abundantly provided with silky hairs than most specimens she has called *H. argenteus,* and agrees well with those she has named *H. fissus.* The latter, however, she does not report from south of Guatemala, and it is moreover excluded by having the upper leaf-surface glabrous, not strongly puberulent as in the Panamanian material. The jumble of characters used to separate *H. argenteus* and *H. fissus* is so inconclusive that the latter is here reduced to synonymy, following Standley and Steyermark in the 'Flora of Guatemala' (Fieldiana: Bot. 24:453. 1946).

1. Holodiscus argenteus (L. f.) Maxim. in Acta Hort. Petrop. 6:254. 1879.

Spiraea argentea L. f. Suppl. 261. 1781.
Spiraea fissa Lindl. in Bot. Reg. 26:Misc. 73. 1840.
Holodiscus fissus (Lindl.) C. K. Schneid. Ill. Handb. Laubh. 1:495. 1905.
Sericotheca fissa (Lindl.) Rydb. in N. Am. Fl. 22:265. 1908.
Sericotheca argentea (L. f.) Rydb. loc. cit. 266. 1908.

Shrub usually 1–3 m. high, with gray-tomentulose branchlets strongly but obtusely angled below the decurrent leaf-bases, the bark on older branchlets reddish-brown, exfoliating in long strips; leaves oblanceolate or the youngest obovate (on vigorous shoots becoming elliptic to ovate, larger than noted here, and with acute or attenuate tips), the upper surface appressed-pilose with hairs up to about 0.5 mm. long, or distally puberulent with much shorter hairs, the lower surface densely floccose-tomentose between the veins and in addition appressed-pilose on the veins with hairs up to 0.7 mm. long, and with similar hairs amid the tomentum; blades

Fig. 65. *Holodiscus argenteus*

mostly 1 cm. or less wide (up to 3 cm.), 2–3 (–6) cm. long, rounded to acute at tip, the basal half entire, cuneate, attenuate to a margined petiole 1–3 mm. long, the margin dentate distally with 4–6 (–8) teeth on each edge, each tooth terminating one of the primary veins of the blade, and tipped by a blunt mucro; veins prominent on both surfaces, strongly impressed above, the primary ones parallel to the sides of the cuneate leaf-base; flowers creamy white, in relatively large paniculiform oblong to pyramidal leafless clusters terminating leafy twigs, the inflorescence mostly 5–15 cm. long, bracteate, often with its lower branches distant and elongate; petals 2–3 mm. long, with an ovate to orbicular entire blade and a short broad claw, pilose with white straight hairs on the outer surface at least near base on midvein; stamens usually 20 (1 opposite each petal and 3 opposite each sepal), the filaments subulate, 1.5–2 mm. long, 0.2–0.3 mm. wide at base, the anthers nearly globose in dried material, about 0.3 mm. long; receptacle shallowly concave, tomentose within but the margin thickened into a fleshy glabrous ring with the stamens inserted on its outer edge, the ring strongly 5-lobed in age; styles with capitate stigmas, in flower ascending and parallel, about 1 mm. long, pilose near base; ovaries flattened, heavily white-pilose with hairs 0.5–0.7 mm. long, especially on the sutures, the sides somewhat hairy or glabrous, but beset with numerous short-stipitate yellowish capitate glands; hypanthium saucer-shaped or hemispheric, 1- to 3-bracteate at base, at maturity about 3 mm. across, the persistent entire triangular sepals 1.5–2 mm. wide at base, 2–3 mm. long; fruit with membranous wall, laterally (i. e., radially) compressed, biconvex, stipitate, the body about 2 mm. long and 1 mm. deep, the inner angle nearly straight from base of stipe to tip

of the persistent style, the outer one abruptly outcurved at base of style, then gradually attenuate into the stipe; total length, including stipe and style, about 3.5–5 mm.

Southern Mexico and Guatemala; Costa Rica and western Panama; Cordillera Oriental, Colombia; highlands in forested areas.

CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, *P. White 58*.

2. HESPEROMELES Lindl.

HESPEROMELES Lindl. in Bot. Reg. *sub pl. 1956*. 1837; Macbr. in Field Mus. Publ. Bot. 13[2]:1065–1069. 1938.

Osteomeles auct., quoad pl. Amer.
Eleutherocarpum Schlecht. in Lechl. Berb. Am. Austr. 59. 1857.

Evergreen shrubs or small trees, sometimes depressed and gnarled, often much branched and the young branchlets often spinose-tipped. Leaves simple, variable in size and shape, mostly coriaceous, 3–5 cm. long or less, crenate or dentate. Flowers 5-merous, pink or white, in small terminal corymbose cymes usually exceeded by the leaves; ovary inferior at anthesis, the 5 carpels distinct from each other from the flowering stage on but attached parietally, at maturity with bony endocarp, enlarged and often somewhat exserted from the fleshy hypanthium; ovule 1 (occasionally 2) in each locule; cotyledons accumbent. Fruit a small red, purple or black pome 1 cm. long or less, tipped by the persistent sepals.

Hesperomeles is a genus of somewhat doubtful standing, scarcely morphologically distinct from *Osteomeles*, of which the (Hawaiian and Chinese) species have pinnate leaves but in technical characters agree precisely with the American *Hesperomeles*. The Old World genus *Pyracantha* is evidently very closely akin to *Hesperomeles*, as evidenced by similarities between species of the two groups, but differs in having the carpels regularly bi-ovulate, and the cotyledons incumbent. A hybrid between *Osteomeles subrotunda* and *Pyracantha crenato-serrata* is known (× *Pyracomeles Vilmorinii* Rehd. ex Guillaumin in Bull. Soc. Nat. Hort. France, VI, 4:191, 198. 1937). Possibly all three of the above genera should be united under the name *Osteomeles* Lindl. (Trans. Linn. Soc. Lond. 13:98. 1821), the oldest name.

About 20 species of *Hesperomeles* have been proposed. These occur in nature at relatively high elevations (mostly above 2000 meters) either in the South American Andes or in the mountains of Panama or Costa Rica. Almost without exception the supposed species have been founded upon leaf characters alone (as witness the names *cordata, cuneata, escalloniaefolia, ferruginea, heterophylla, latifolia*, etc.). A study of the available herbarium material indicates that no general correlation is possible between leaf characters and those of the inflorescences. The flowers and fruits, inflorescences, types and distribution of pubescence, venation-patterns, and occurrence of spinescent branching are very nearly identical in all

the supposed species within reasonable limits of variation—as nearly identical as would be expected in any genus which had long evolved not in a continuous geographical range but on the series of isolated areas which are the *páramos* and *subpáramos* of the Andes. The differences between the leaves of the supposed species of *Hesperomeles* are correlated in a very general way with habitat and with vigor of the plant itself; in other words the large-leaved plants, which are usually those with most vigorous apical growth of the branches, occur mostly at lower elevations under relatively mild climatic conditions. These differences in leaf characters are doubtless now transmitted genetically, even though they may reflect the effect of environments of past geological periods. Apparently many local races have developed, but as these vary so much as to defy precise definition, as they differ in such trivial ways and are all fundamentally so much alike morphologically, it would seem unwise to dignify them by calling them species, especially since such a course would entail the naming of many more than have already been so treated. A treatment that seems to be more in accord with the biology of the group is to consider most of the plants as belonging to a single wide-ranging species with numerous local races (subspecies, varieties, forms, ecotypes, apomictic strains, or whatever other categories further field study may suggest). These local races are of unknown phylogenetic or systematic position and should not be given formal Latin names until their interrelationships and exact distributions have been worked out.

The Panamanian member of this group is a small-leaved race indistinguishable morphologically from races of the higher Andes in Colombia, Ecuador, Peru, and Bolivia. It appears to be conspecific with the slightly more vigorous and larger-leaved race which was illustrated by Ruiz and Pavón as *Mespilus heterophylla*, and it is treated here as belonging to that species.

1. HESPEROMELES HETEROPHYLLA (R. & P.) Hook. Ic. Pl. 9:*pl. 846.* 1852.

Mespilus heterophylla Ruiz & Pav. Fl. Peruv. 4:*pl. 425b.* 1802.
Mespilus lanuginosa Ruiz & Pav. loc. cit. 4:*pl. 425a.* 1802.
Osteomeles obovata Pittier in Contr. U. S. Nat. Herb. 20:108. 1918.
Hesperomeles obovata (Pittier) Standl. in Field Mus. Publ. Bot. 18:480. 1937.
Hesperomeles chiriquensis Woodson in Ann. Mo. Bot. Gard. 26:288. 1939.

Evergreen shrub or small tree up to 5–6 m. high, the smaller forms at higher elevations usually intricately branched, the branches often spinescent; bark on the older branches gray; branchlets reddish-brown with prominent pale lenticels, when young covered with pale or (usually) lustrous reddish-brown hairs about 0.5 mm. long, the hairs contorted at base and curved into a hook or a closed loop, but with their distal ends appressed toward the tips of the branchlets; bark of the branchlets ultimately glabrescent but much roughened by the persistent raised bases of the deciduous hairs; leaves coriaceous, obovate or oblanceolate to elliptic, the blades lustrous and rugose-reticulate above, paler beneath, with a prominulous network of veins, rounded to acute at tips, usually cuneate at base, mostly 1.5–2.5 (–4.5) cm. long and 0.5–1.5 (–2.5) cm. wide, varying from about 2–3 times as long as

wide (on vigorous shoots and especially near tips of branches) to about 1–1.4 times as long as wide (on depressed and much-branched plants with little apical growth, and especially near the bases of branchlets); petioles 1–4 mm. long; stipules subulate, 0.5–0.7 mm. long, early deciduous; blades glabrous or nearly so beneath, often glabrate above but usually with some pale or reddish hairs persistent at least near base in the groove formed by the sunken midvein; margins dentate except near base, with 8–11 low rounded teeth on each edge, the teeth at first tipped with minute glandular processes; flowers in small corymbose cymes terminating the leafy branches, the cymes pubescent and later roughened like the branches, with about 20 flowers or fewer, up to about 3 cm. across, the lower branches up to about 3 cm. long, all the branches bracteate, the bracts like reduced leaves but very narrow, mostly 3–6 mm. long, 0.3–1 mm. wide, very acute at both ends; flowers with a "strong, sweet scent" (E. K. Balls), on pedicel-like cyme-branches 1–3 mm. long, or essentially sessile; petals white or pale pink, or white with pink margins, obovate-oblong, concave, erose-denticulate, glabrous, or pilose on the midline without, rounded at apex (sometimes cuspidate), mostly 3.5–5 mm. long and 3–4 mm. wide, narrowed at base to a stout claw 1 mm. wide; stamens 20, the filaments narrowly triangular, flat, about 1.5–3 mm. long, the anthers pink or rose-colored, about as broad as long, 0.7–1.3 mm. long; disk white- or rufous-tomentose, varying to almost glabrous; styles 5, filiform, 4–5.5 mm. long, distinct to the base but approximate, arising from the inner angles of the carpels, white-pilose for 1–2 mm. at base; stigmas terminal, capitate, about 0.3 mm. across, often slightly oblique; hypanthium in anthesis campanulate or turbinate, 3–5 mm. long, the apex truncate and surmounted by the 5 broad-based calyx-lobes which are 2–3 mm. wide at base, 2.5–4 mm. long, deltoid, or with a subulate tip; hypanthium and calyx-lobes vestite like the branches of the cymes, or the lobes glabrous at least toward tips; fruit red, or nearly black when ripe, globose to oblong, fleshy (in some races said to be edible), glabrescent, up to 1 cm. long, the styles and calyx persistent; pyrenes 4–4.5 mm. long.

Costa Rica and Panama; Colombia and Venezuela to Bolivia; thickets, open hillsides, and páramos, mostly at elevations greater than 2000 meters.

CHIRIQUÍ: Potrero Muleto, Volcán de Chiriquí, *Davidson 1055;* Cerro Pando, valley of the upper Río Chiriquí Viejo, *P. White 43;* Loma Larga to summit, Volcán de Chiriquí, *Woodson, Allen & Seibert 1078.*

3. RUBUS L.

By L. H. BAILEY

Rubus L. Gen. Pl. ed. 5, no. 557. 1754.

Woody plants, erect or trailing or somewhat climbing, bearing flowers and fruits on canes of the second year; in the first year the growths from the root are called primocanes, and in the second year are known as floricanes when they bear fruit and perish; axes usually bear sharp prickles, and often hairs and stalked

glands; leaves (in the known Panama species) 3-foliolate or 5-foliolate except sometimes a few of them simple in the inflorescence, frequently more or less persisting until the following year; inflorescence racemiform or paniculiform, axillary and usually terminating the canes, pedicels often lengthening in fruit; flowers perfect and complete (in our species); calyx 5-lobed, sometimes glandiferous; petals 5, distinct; stamens numerous, surpassing the head of many small closely packed pistils; fruit a syncarp composed of small simple coherent drupelets that are either attached as a body to the receptacle (blackberries) or forming a cap (raspberries) that falls intact from the receptacle.

Hundreds of species in many parts of the world, particularly in the North Temperate Zone, in the tropics usually on higher lands and mountains.

The brambles of Panama are not yet fully collected or well understood, and some of the identifications are subject to modification. Good complete specimens are needed to verify the determinations, with both primocane and floricane parts from the same plant, together with notes on stature and habit.

I. *Blackberries.* Fruit (syncarp) composed of drupelets that adhere to receptacle and the aggregation falling as one body or "berry"; drupelets rather large, mostly loosely aggregated; main stems or axes usually angled or furrowed, neither glossy or pruinose.
  a. Axes of canes and inflorescence not hairy or hispid or setose, more or less closely pubescent; fruits pendent ..... 1. R. PANAMANUS
  aa. Axes prominently hairy or hispid or setose; fruits erect.
    b. Canes beset with glandiferous hairs ..... 2. R. PRAECIPUUS
    bb. Canes not glandiferous.
      c. Leaflets abruptly contracted into very narrow apex; canes pubescent but not densely long-hairy; prickles many; clusters very dense ..... 3. R. TANTUS
      cc. Leaflets gradually acuminate, somewhat pubescent; canes thickly shaggy; prickles few; clusters open ..... 4. R. TRICHOMALLUS

II. *Raspberries.* Fruit a cup of drupelets separating from the receptacle (which remains on the plant); drupelets small, much compacted; main stems or axes usually evenly terete, polished and mostly pruinose ..... 5. R. GLAUCUS

1. RUBUS PANAMANUS Bailey, in Gent. Herb. 6:355. 1944.

Diffuse and scandent; canes whitish-pubescent, with few and scattered hooked prickles; primocane foliage not recorded; floricane leaves minutely pubescent on upper surface, pubescent-tomentulose on veins underneath, finely and sharply serrate, 3-foliolate or perhaps simple in the inflorescence; leaflets narrow-elliptic, terminal or central one 8–10 cm. long, 4–5 cm. broad, narrowed to long point; flowers a dozen or fewer in axillary and one terminal racemiform open cluster; corolla 1 cm. or less across, white; pistils dark-colored; fruit pendent, about 1 cm. long; drupelets many and closely packed.

Panama.

CHIRIQUÍ: Bajo Chorro, Boquete Distr., 2000 m., *Davidson 72.*

This plant has been called *R. alpinus* Macf., a species native in Jamaica but not known in Panama.

2. Rubus praecipuus Bailey, in Gent. Herb. 6:356. 1944.

Large bramble, canes sometimes 5 m. long, densely and finely pubescent and covered with brownish glandular hairs, and bearing scattered broad-based hooked prickles; primocanes not recorded; leaves of floricanes large, minutely hairy on upper surface, softly pubescent underneath, sharply minutely serrate, 3- to 5-foliolate; leaflets oblong-acuminate to elliptic-acuminate, 8–11 cm. long, 4–6 cm. broad; petiole glandular-hairy; inflorescence terminal, panicle-like, 20–30 cm. long, central rachis continuous, glandular-hairy; flowers white to pink, 2–2.5 cm. across; fruit oblong, 2 cm. or less long, very seedy.

Panama.

chiriquí: Quebrada Velo, 1800 m. alt., *Woodson & Schery 275;* vicinity of Casita Alta, Volcán de Chiriquí, 1500–2000 m. alt., *Woodson, Allen & Seibert 801, 869.*

3. Rubus tantus Bailey, in Gent. Herb. 6:361. 1944.

Upright and stout, canes pubescent but not long-hairy or shaggy, prickles many and recurved, not glandular; leaves somewhat pubescent on upper surface, gray-tomentose on under surface, closely sharply serrate, 3- to 5-foliolate; leaflets ovate to ovate-elliptic, sometimes subcordate, 7–9 cm. long, about 4 cm. broad; petiole pubescent and prickly; inflorescence terminal and short, panicle-like, lateral clusters in upper axils; flowers many, crowded, small, pinkish-white; fruit small, with few drupelets.

Panama.

chiriquí: vicinity of El Boquete, 1000–1300 m., *Maxon 5107;* pastures, *Pittier 3127.*

4. Rubus trichomallus Schlecht. in Linnaea 13:268. 1839.

Vigorous, large, 2 m. high, the canes shaggy brown-hairy but not glandular, closely pubescent on surface, prickles remote and hooked; primocane leaves many and large, puberulent on upper surface, grayish-tomentose on under surface, finely and unevenly sharp-serrate, 3- to 5-foliolate; leaflets narrowly ovate-elliptic-acuminate, 8–10 cm. long, 3–5 cm. broad, sometimes subcordate; petiole stout, hairy-pubescent, aculeate; inflorescence panicle-like and terminal with a few smaller clusters in upper axils, the peduncles brown-hairy and commonly prickly; flowers white, small, about 1 cm. across; fruit small, short-oblong, about 1 cm. long.

Southern Mexico to Panama, but the identity of the Panama plant not yet clear.

chiriquí: Cerro Vaca, in forest or thickets, 900–1136 m. alt., *Pittier 5721;* pastures around El Boquete, 1000–1300 m., *Pittier 3139;* vicinity of El Boquete, *Maxon 4927.* coclé: vicinity of El Valle, *Allen 1189, 1647, 1776.*

5. Rubus glaucus Benth. in Plant. Hartweg. 173. 1839. "Black Raspberry."

Diffuse or erect, to 1.5 m. tall; primocanes smooth, glaucous, with uncinate scattered prickles 2–3 mm. long; leaves dull green, glabrous on upper surface, gray-tomentose underneath, minutely serrate, 3-foliolate; leaflets elliptic-ovate to ovate-lanceolate, 6–10 cm. long, long-acuminate, petiole with hooked prickles; flowers mostly solitary, sometimes 2 or 3, in upper axils; corolla white sometimes tinged

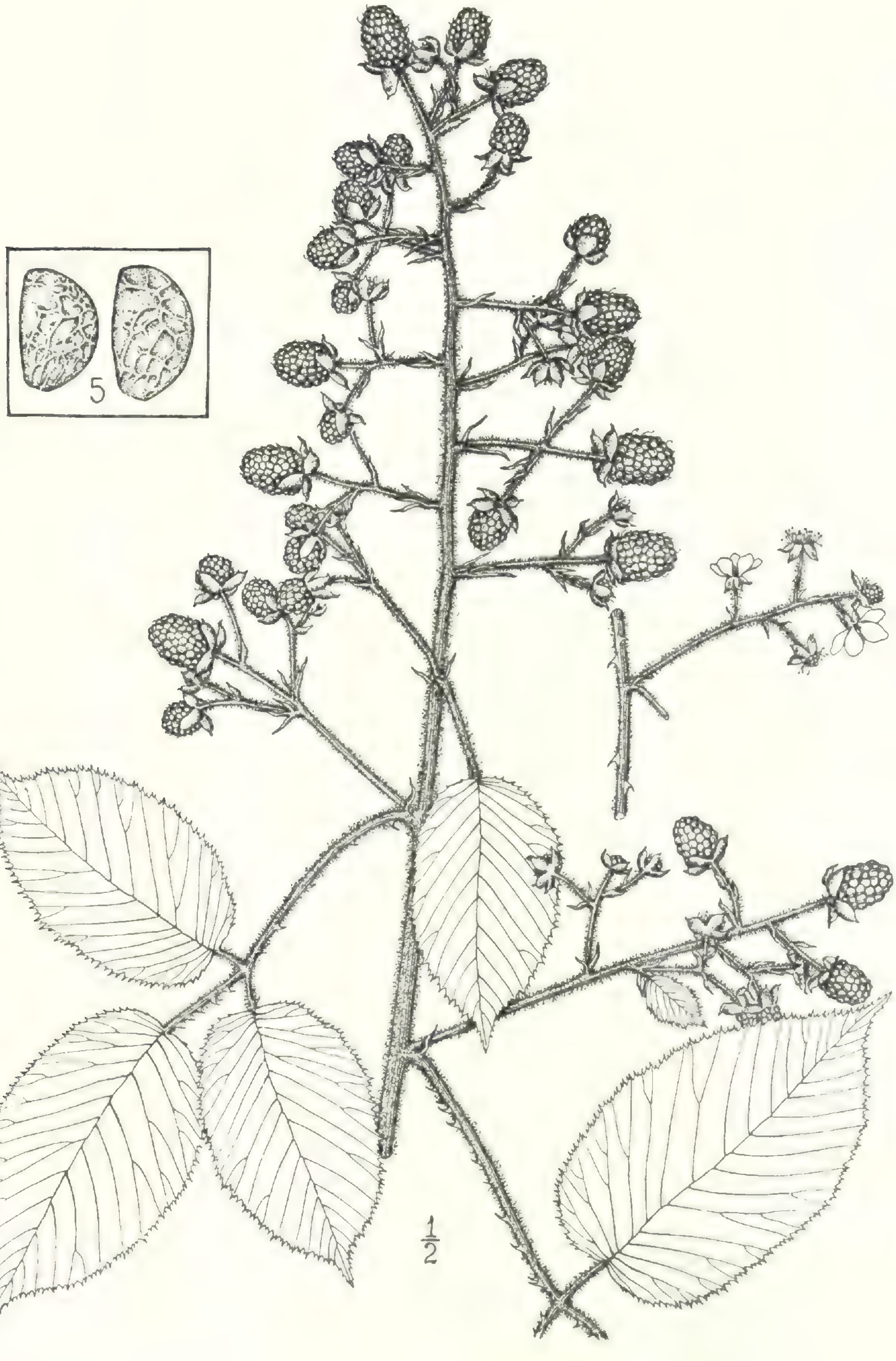

Fig. 66. *Rubus praecipuus*

Fig. 67. *Rubus trichomallus*

green, about 1.5 cm. broad; fruit oblong or thimble-shaped, 1.5 cm. and more long, becoming black, of good quality.

Panama, Colombia, Ecuador.

CHIRIQUÍ: Volcán de Chiriquí, Loma Larga to summit, 2500–3880 m. alt., *Woodson, Allen & Seibert 1081;* vicinity of Cerro Punta, 1500–2000 m., *Seibert 264;* llanos de volcán, about 1300 m., *Allen 1546;* El Boquete, 1000–3000 m., *Pittier 3135.*

4. ALCHEMILLA L.

ALCHEMILLA L. Gen. Pl. ed. 5, 58. 1754; L. M. Perry in Contr. Gray Herb. 84:1–57. 1929.

Alchemilla, sect. *Lachemilla* Focke, in Engl. & Prantl, Nat. Pflanzenfam. 3^3:43. 1894. *Lachemilla* (Focke) Rydb. in N. Am. Fl. 22:380. 1908.

Perennial herbs, often prostrate or procumbent, often stoloniferous. Leaves alternate, petiolate, usually palmately lobate or cleft, the upper smaller, with fewer lobes or divisions, sessile; stipules sheathing, usually foliaceous, lobed or cleft, adnate to the petiole, the whole often appearing as a multifid perfoliate leaf or a many-lobed sheath. Flowers minute, usually crowded into small axillary or terminal glomerulose cymes, less often in loose racemoid inflorescences; hypanthium persistent, urceolate, the 8–10 lobes 2-seriate, the outer ones smaller; petals none; stamens 1–4, free, opposite the calyx-lobes, the filaments short, usually not more than half the length of the calyx-lobes; disk with thickened margin, nearly closing the mouth of the hypanthium. Fruit of 1–6 achenes, these sessile or stipitate, included in the hypanthium, with basal, ventral, ascending and persistent styles, and capitate or clavate stigmas.

This group of species, whether it be treated as a genus, *Lachemilla,* as done by Rydberg and more lately by Rothmaler (Fedde Rep. Sp. Nov. 42:164–173. 1937), or as a section or subgenus of *Alchemilla,* following Focke, Miss Perry, and more recent American authors including Standley (Field Mus. Publ. Bot. 18:477–478. 1937), and Standley & Steyermark (Fieldiana: Bot. 24:436–440. 1946), is easily recognized in the field, but the individual species are difficult of interpretation. The flowers are very small (3–4 mm. long or less), and in consequence the species have been distinguished chiefly by the use of characters of leaf-shape and lobing, distribution and quality of pubescence, and other vegetative characters which are not always convincing. Miss Perry divided the group as a whole into six easily recognizable series, or species-groups, of which two, the ORBICULATAE and the APHANOIDES, are represented in Panama.

a. Basal leaves 5- to 11-lobed or -cleft, the blades relatively broad and merely toothed, even those of the upper leaves much broader than and distinct from the stipules.
  b. Leaf-blades shallowly 5- to 11-lobed ..... 1. A. ORBICULATA
  bb. Leaf-blades palmately 5- to 9-cleft to near their bases ..... 2. A. PASCUORUM
aa. Basal leaves 3- to 5-cleft or -parted, the blades with narrow finger-like lobes, those of the upper leaves often similar to and little exceeding the stipules ..... 3. A. APHANOIDES

1. Alchemilla orbiculata Ruiz & Pav. Fl. Peruv. 1:68. 1798.

Alchemilla pectinata HBK. Nov. Gen. & Sp. 6:226. 1824; Perry in Contr. Gray Herb. 84:14. 1929.
Lachemilla orbiculata (R. & P.) Rydb. in N. Am. Fl. 22:381. 1908.

The stolons usually with well-developed leaves bearing offsets or floral shoots in their axils; basal and lower stem-leaves orbicular-reniform, 1.5–4 cm. broad, stiff, deeply cordate, the lobes serrate; blades green and glabrate above, appressed-silky beneath, the surface beneath the silky hairs glaucous with minute waxy particles; petioles sericeous, 3–6 (–20) cm. long; stipules of the upper leaves foliaceous, forming a somewhat tubular sheath, deeply incised, the lobes not spreading nor recurving; inflorescence racemose, often terminal and 4–6 cm. long in Panamanian material seen; flowers relatively large, at maturity 3.5–4 mm. long, densely silky; achenes 2–4.

Since the publication of Miss Perry's revision, American botanists generally have treated *Alchemilla pectinata* HBK. as a species distinct from the South American *A. orbiculata*, which differs in having greatly reduced or scale-like leaves on the stolons, sheathing (not merely amplexicaul) bracts subtending the flowers, and 1–2 (not 4–6) carpels. These differences do not seem to be greater than might be expected in geographically separated races of the same species, and in this case I prefer to accept the judgment of Rydberg, who could usually be depended upon to find differences between species whenever such differences existed.

Central Mexico to Bolivia, at the higher elevations, usually above 2000 meters, in clearings and on the *páramos* of the Andes.

Chiriquí: Loma Larga to summit, Volcán de Chiriquí, *Woodson, Allen & Seibert 1042;* Potrero Muleto to summit, *Woodson & Schery 401, 438.*

2. Alchemilla pascuorum Standl. Jour. Wash. Acad. 17:310. 1927.

Lachemilla pascuorum (Standl.) Rothm. in Fedde Rep. Sp. Nov. 42:171. 1937.

Basal and lower stem-leaves orbicular-reniform, 2–4 cm. broad, the lobes cuneate-obovate, rounded at apex, incised-dentate above the middle, green and sparingly pilose above, densely to sparsely appressed-silky beneath, the surface beneath the silky hairs glaucous with minute waxy particles; petioles 2 cm. long or less, appressed-pilose; stipules of the upper leaves foliaceous, forming a short sheath, deeply incised, the lobes spreading or recurving; inflorescences compact, in short axillary clusters or racemes 2–4 cm. long; flowers 2–2.5 (–3) mm. long, densely silky; achenes 2–4.

Possibly not to be distinguished specifically from *Alchemilla venusta* Schlecht. & Cham. (of Mexico), *A. guatemalensis* Rothm. (Guatemala), or *Lachemilla fulvescens* (Perry) Rothm. (Colombia). Perry separates *A. venusta* from *A. pascuorum* on the basis of its "villous, turbinate-urceolate" (not "sericeous, globose-urceolate") hypanthium, and its erect to spreading (not erect to subconnivent as

Fig. 68. *Alchemilla pascuorum*

in *A. pascuorum*) calyx-lobes. I find these characters difficult of interpretation and think the species rather too close together.

As pointed out by Perry, *Alchemilla pascuorum* is also closely related to *A. pectinata (orbiculata)*. All the Panamanian material I have been able to examine falls into two rather well-defined groups, one with relatively large basal leaves often 2.5–3 cm. broad, and a distinct erect terminal racemose inflorescence 4–6 cm. long. The other group has the basal leaves somewhat more deeply divided (but not always to near the base), mostly 1.5–1.8 cm. broad, and the flowers in shorter clusters, 2–4 cm. long, from the axils of the well-developed stolons. The first group, with the larger leaves, undoubtedly represents *Alchemilla orbiculata*. The second I have here called *A. pascuorum*, although at least one of the specimens cited below as this species has been seen by Miss Perry and cited, with some doubt, as *A. pectinata* (*Woodson et al. 892*, cited in Ann. Mo. Bot. Gard. 26:287. 1939).

CHIRIQUÍ: Volcán de Chiriquí, Cerro Copete, *Allen 4858;* Chiquero, Boquete Distr., *Davidson 546;* Cerro Pando, valley of the upper Río Chiriquí Viejo, *P. White 8;* Volcán de Chiriquí, Casita Alta, *Woodson, Allen & Seibert 892.*

3. ALCHEMILLA APHANOIDES L. f. Suppl. 129. 1781; Perry in Contr. Gray Herb. 84:36. 1929.

Alchemilla hirsuta var. *alpestris* Cham. & Schlecht. in Linnaea 5:572. 1830.
Alchemilla subalpestris Rose, in Contr. U. S. Nat. Herb. 10:96. 1906.
Lachemilla tripartita (R. & P.) Rydb. in N. Am. Fl. 22:383. 1908.
Lachemilla subalpestris (Rose) Rydb. loc. cit. 384. 1908.
Alchemilla aphanoides var. *subalpestris* (Rose) Perry in Contr. Gray Herb. 84:39. 1929.
Lachemilla aphanoides (L. f.) Rothm. in Fedde Rep. Sp. Nov. 42:170. 1937.

Stems erect to decumbent, subsimple or branched, densely to sparsely pilose; leaves tripartite, the lower more densely pubescent than the upper, the segments oblanceolate to cuneate-obovate, multifid or incised-dentate; stipules foliaceous, 2- to 4-lobed or cleft, often with the sessile upper leaves forming many-lobed or

perfoliate "leaves"; flowers aggregated in small axillary and terminal cymes, usually very short-pedicellate; hypanthium glabrous or nearly so at least at maturity, the outer lobes about equalling the inner; flowers in Panamanian material less than 2 mm. long; achenes 1–3.

Northwestern Mexico to Bolivia; mountains, often at elevations between 2000 and 3000 meters, in clearings and on *páramos*.

The North American representatives of this species have lately been referred to var. *subalpestris*, which has somewhat shorter flowers than the typical variety and is somewhat less pubescent except for the hypanthium, which may be sparsely hairy in the Panamanian plant. *Alchemilla aphanoides* is very closely related to *A. sibbaldiaefolia* HBK., but the Central American representatives of the latter are marked by rather strongly pubescent hypanthia, and I have not seen any such from Panama.

CHIRIQUÍ: Volcán de Chiriquí, Potrero Muleto, *Davidson 1040;* Loma Larga to summit, *Woodson, Allen & Seibert 1041;* Potrero Muleto to summit, *Woodson & Schery 418*.

5. ACAENA L.

ACAENA Mutis, ex L. Mant. Pl. 145. 1771; Bitter, in Bibl. Bot. 74:1–336. 1910–1911.

Herbaceous or low suffrutescent plants usually with odd-pinnate leaves, toothed leaflets, and stipules more or less adnate to the petioles. Flowers in spikes or racemes, apetalous, the sepals and stamens variable in number (usually 4); pistil usually 1 with short terminal style and multifid stigma, at maturity forming an achene wholly inclosed in the prickly hypanthium.

1. ACAENA ELONGATA L. Mant. Pl. 200. 1771.

Acaena agrimonioides HBK. Nov. Gen. & Sp. 6:231. 1824.

Plants shrubby at base, often with upright herbaceous branches, about 1 m. high or less, the bark on the older branches exfoliating in very thin reddish-brown sheets; plant ultimately glabrate, but juvenile stems and leaves vestite with loosely appressed silky straight yellowish-white hairs 0.7–1.5 mm. long. Leaflets often 13 (9–19 according to Bitter), the proximal ones much reduced in size, the 7 distal ones all alike (or the terminal one slightly larger), elliptic or oblong to obovate, often 5–8 mm. wide, 10–20 mm. long, acute at each end or obtuse at tips, the two edges very unequal at base, the proximal edge of at least the terminal pair decurrent on the rachis, the petiolules mostly 1–2 mm. long; margins of leaflets rather coarsely crenate-serrate with 6–8 teeth on each edge, the teeth often pilose-tufted; stipules adherent to the rachis, scarious, often reddish-brown, connate at base and forming a sheath 1–2 mm. long about the stem, thence tapering gradually toward tips, the body 5–15 mm. long, the free herbaceous tips linear, entire, 2–6 mm. long; margins of stipules, rachis and sometimes axis of inflorescence with scattered stipitate glands; pubescence of leaf at maturity often reduced to

Fig. 69. *Acaena elongata*

tufts at bases of leaflets, on upper side. Flowers racemosely arranged on leafless axillary branches mostly 20–30 cm. long, relatively few (often 8–10) to a branch, each borne on a short lateral bracteate branchlet (up to 1.5 cm. long, or most often 1 mm. long or less) which is bibracteolate at summit and terminated by a pedicel 1–4 mm. long; calyx-lobes 4, green (contrasting with the reddish hypanthium), ovate, acute, about 1 mm. wide and 1.5 mm. long, at anthesis crowning the flower and much exceeding the spines of the hypanthium, but at maturity immersed in the spines; stamens 3–4, purplish, 1–2 mm. long, the anthers reniform, 0.5 (–0.8) mm. long and about 1.2 mm. wide after dehiscence; style very short, tipped by the expanded flattened peltate stigma which is about 1.5 mm. broad, bilateral, the divisions deeply lacerate; hypanthium in anthesis cylindric, reddish, at maturity pendent, broadly ovoid or ellipsoid to globose, 3–5 mm. in diameter and 5–8 mm. long (exclusive of spines), the outer layer inflated, membranaceous, glabrous or puberulent; spines uniformly distributed, spreading, arising from the 10–12 ribs of the hypanthium (about 6 to each rib) which are concealed by the outer inflated layer; visible part of the spines 2–3 mm. long, purplish-red or brown, commonly with 3 retrorsely pointed barbs at apex.

Central Mexico to Guatemala; Costa Rica and Panama; Colombia and Ecuador; open meadows, thickets or wet forests, in highlands, mostly at elevations of 2000 meters or above, sometimes becoming a noxious weed.

CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, *P. White 62*.

6. PRUNUS L.

PRUNUS L. Gen. Pl. ed. 5, 213. 1754; Koehne in Engl. Bot. Jahrb. 52:279–333. 1915; Macbride in Field Mus. Publ. Bot. 13[2]:1083–1090. 1938.

Trees with alternate simple leaves. Flowers (in Panamanian species) white, racemose; calyx 5-lobed, the tube perigynous, cup-like, forming with the receptacular disk the hypanthium bearing the 15–20 stamens and 5 petals at its margin; filaments free, filiform or somewhat dilated at base; carpel 1, with terminal style and peltate or truncate stigma; ovules 2, collateral. Fruit a drupe, one-seeded, often with juicy pulp.

A large genus, best known for the numerous species which are cultivated for food and for ornament. Segregate genera, e. g. *Padus* and *Laurocerasus,* are maintained by some botanists but are based chiefly on characters of the inflorescence and are probably best included in *Prunus*. The native Panamanian species belongs to the Section LAUROCERASUS as defined by Koehne in 1915. This author included 47 species in the section, 42 of them American. At the time of his revisionary studies Koehne was unable, because of lack of material, to integrate the results of his studies in the several distinct floristic areas in tropical and subtropical America, and it is probable that the actual number of species will prove smaller than his estimate. In the area including Mexico and Central America Koehne recognized 7 species, of which he described 5 as new. The characters used by him to distinguish species in the group to which the Panamanian plant apparently belongs (i. e. the species having entire leaves, glabrous petals, solitary racemes, and superficial glands near the base of the leaf blade), appear to be of little value for this purpose. The number of glands on the leaf-blade, which was assumed by Koehne to be constant for a species, varies from 0 to 3 on either side of the midrib of the same leaf, and from 0 to 4 (rarely 6) on different leaves on the same plant. The unusual development of lenticels and the transverse cracks in the branchlets, on which he based *Prunus tuberculata* and *P. annularis*, respectively, do not appear to be constant characters. After study of somewhat more material than was available to Koehne, I doubt that more than one species exists in this group, at least in Central America. The oldest name which is applicable to the species is *Prunus brachybotrya* Zucc. (1837), from Mexico, but pending a revision of the whole group it seems wisest at present to refer the Panamanian plant to a species originally described from nearby Costa Rica, *Prunus annularis*.

Fig. 70. *Prunus annularis*

1. PRUNUS ANNULARIS Koehne in Engl. Bot. Jahrb. 52:308. 1915.

Large evergreen tree, up to 20 m. tall with trunk up to 50 cm. in diameter, entirely glabrous. Leaves coriaceous, entire, elliptic to lanceolate or ovate, 2.5–5.5 cm. wide, 6–13 cm. long, usually 2–2.5 times as long as wide, rounded at base, narrowed toward the apex from about the middle, with a short blunt acumen; petiole stout, 1–1.5 mm. in diameter, 1–1.5 cm. long; lateral veins often 5–7 pairs, inconspicuous, slender, arcuate-ascending, anastomosing well inside the margin; glands usually present on the lower surface of the blade near base, round or oval, often about 0.5 mm. wide and 0.7 mm. long, 1–2 (rarely none, or 3) on each side of the midrib, mostly 5–10 mm. from the base of the blade and about 5 mm. from the margin, but sometimes as little as 1–2 mm. from base or margin; stipules very soon deciduous, not seen, probably narrowly linear, 2–4 mm. long. Flowers in leafless racemes 4–5.5 (–7) cm. long, these from the axils of the subpersistent leaves of the preceding season; flowers 20–40, subtended by very small chartaceous bracts which are deciduous before the flowers open; pedicels naked, 3–7 mm. long (those at the base of the racemes the longest), 0.5–0.7 mm. in

diameter at anthesis, up to 1.5 mm. in diameter in fruit, mostly at right angles to the axis; petals white, glabrous, entire, rounded or reniform, about 2 mm. long including the short claw, 2–2.5 mm. wide; stamens about 20, glabrous, the filaments 2.5–4 mm. long, subulate; anthers (0.6?–) 0.7–1 mm. long, elliptic; hypanthium in anthesis campanulate, about 3 mm. broad and high, the calyx-lobes broadly triangular, blunt or acute, about 1.5 mm. wide at base, 1 mm. long, entire; hypanthium and calyx deciduous immediately after anthesis; ovary glabrous, about 1.5 mm. long, tipped by the straight style 2–3 mm. long and 0.3 mm. in diameter; stigma peltate, 0.7–0.9 mm. across. Fruit probably a purple ovoid drupe with thin flesh, about 1.5 cm. in diameter, 2 cm. long; stone ovoid, pointed, about 10 mm. in diameter, 13 mm. long; seed globose, about 9 mm. in diameter.

Costa Rica and Panama; related species or perhaps the same species from Vera Cruz and Chiapas through Central America into northern South America; chiefly in rain forests, at elevations from 1000 to 2000 meters.

CHIRIQUÍ: Bajo Chorro, Boquete Distr., *Davidson 235;* between El Volcán and Cerro Punta, *G. White 14;* vicinity of Casita Alta, Volcán de Chiriquí, *Woodson, Allen & Seibert 907.*

Prunus occidentalis Sw., reported from the Volcán de Chiriquí by Seemann (Bot. Voy. Herald, 119. 1852–53), is a West Indian species not known to occur in Panama; the report was doubtless based on what is here called *Prunus annularis*. *Prunus cornifolia* Koehne, a Costa Rican species recognized by having a persistent calyx and tufts of hairs in the axils of the main foliar veins (Sect. NEOCALYCINIA Koehne), was erroneously reported from Panama (Ann. Mo. Bot. Gard. 27:312. 1940), but its known range is from southern Mexico to Costa Rica only. The common half-wild cherry of the highlands of Guatemala and southern Mexico, the *capulín, Prunus capuli* Cav., has apparently not been reported from Panama, although it is widely naturalized from Venezuela to Bolivia. It may be recognized by the racemose inflorescence which bears leaves near its base, the crenate-dentate leaves bearing reddish hairs beneath along the midvein, the persistent calyx and the sweet nearly black juicy fruit 1–1.5 cm. in diameter.

7. CHRYSOBALANUS L.

CHRYSOBALANUS L. Gen. Pl. ed. 5, 229. 1754.

A small (possibly monotypic) genus of shrubby plants with entire coriaceous leaves. Flowers white, in axillary cymes; calyx (hypanthium) perigynous, the lobes 5; petals 5; stamens about 20, hirsute, coherent; ovary sessile at the bottom of the hypanthium; ovules 2; style basal. Fruit a drupe with one bony stone having 5–6 angles.

1. CHRYSOBALANUS ICACO L. Sp. Pl. 513. 1753; Hook. f. in Mart. Fl. Bras. 14^2:7. 1867.

Low shrub 1–2 m. high, or prostrate, or a medium-sized tree up to 5–6 m. high, glabrous or essentially so except in the inflorescence and on very young

Fig. 71. *Chrysobalanus Icaco*

growth, where strigose; bark of the branchlets reddish-brown, smooth except for the very numerous and conspicuous pale lenticels. Leaves varying considerably from one plant to another, elliptic to obovate or suborbicular, rounded or emarginate at apex or when elliptic narrowed to an obtuse apex, cuneate to acute or rounded at base, up to about 8 cm. long and 6 cm. wide, (1–) 1.5–2 times as long as wide, on stout petioles 2–4 mm. long; blades dark green and lustrous above, dull beneath and usually with a depressed elliptic glandular area about 0.5 mm. long on each side of the midrib at extreme base; small veins prominently reticulate on both sides of the blade, the primary lateral veins mostly 4–6 pairs, straight at base but curving and anastomosing before reaching the margins. Flowers white, in short-peduncled axillary cymes shorter than the leaves (mostly 2–4 cm. long, with 8–20 flowers), the cyme-branches often strongly flattened and 1–1.5 mm. wide, often glabrescent near the base, the tips densely pale-strigose like the hypanthium, the flowers and the tips of the cyme-branches appearing silvery white to the unaided eye; cymes usually naked in anthesis, the ovate, acute, finely glandular-ciliate bracts 1.5–2 mm. long but very soon deciduous; petals 5, glabrous, oblanceolate or spatulate, 3–5 mm. long, 2–3 times as long as wide, the tips rounded, often erose, the bases cuneate; stamens about 20 (up to 30, according to Hooker) in one series, the filaments pale (?white), about 5 mm. long or less, hirsute on the inner surface except on the distal third, the flattened bases coherent a third or half the length of the filaments into a cylinder; anthers about 0.5 mm. long, ?pink or ?purplish; hypanthium campanulate or turbinate, at anthesis about 3 mm. long and wide, the inner surface hairy, the long-hirsute ovary sessile at the bottom of the tube, the filiform style 6–7 mm. long, hirsute except at tip, erect, with a minute terminal stigma; calyx-lobes triangular-ovate, acute or blunt-tipped, heavily pubescent, the margins glandular-ciliate but otherwise entire. Fruit globose or oval, 2–5 cm. long, white to pink or purple, edible, with white juicy insipid flesh, the stone 1–2 cm. long with 5–6 acute longitudinal ribs.

Tropical America, from Florida and Tamaulipas southward through the West Indies and Central America to northern Brazil and to Ecuador; tropical West Africa; near sea level, in beach thickets and coastal swamps; often planted inland.

BOCAS DEL TORO: Nances Cay, vicinity of Chiriquí Lagoon, *von Wedel 2936*. CANAL ZONE: Aspinwall, *Hayes 636*; Chagres, *Fendler 107*. COCLÉ: Penonomé, *Williams 400*. COLÓN: Manzanillo Island, *Hayes 709*. PANAMÁ: San José Island, [*Johnston, Erlanson*].

8. LICANIA Aublet

Licania Aubl. Hist. Pl. Guian. Fr. 119, *pl. 45*. 1775; Hook. f. in Mart. Fl. Bras. 14^2:8–19. 1867; Fritsch, in Ann. K. K. Naturhist. Hofmus. Wien 4:33–60. 1889.

Moquilea Aubl. loc. cit. 521, *pl. 208*. 1775; Hook. f. in Mart. Fl. Bras. 14^2:19–26. 1867; Focke in Engl. & Prantl, Nat. Pflanzenfam. 3^3:58. 1894.

Trees with alternate simple entire leaves. Flowers usually paniculate, the ultimate branchlets cymosely branched; hypanthium globose or campanulate, the lobes 5; petals 5, minute or none; stamens 3 to many, inserted at the margin of the hypanthial disk, often connate at base, forming a complete ring or unilaterally disposed; ovary unilocular, sessile at the bottom of the hypanthium, hairy; style basal; fruit drupaceous, various, one-seeded, the pericarp usually leathery or woody.

a. Leaves tomentose beneath with fine white or nearly white appressed tomentum.
  b. Leaves broadly rounded at apex, obtuse or (usually) subcordate at base, mostly 1.4–1.7 times as long as wide; branchlets stout, often 3–6 mm. thick at base of inflorescence; stamens about 20 ..... 1. L. ARBOREA
  bb. Leaves acute or acuminate at apex, acute to rounded at base, mostly 2–2.7 times as long as wide; branchlets at base of inflorescence slender, 1–2 mm. thick; stamens 3 (sometimes in addition to a few vestigial rudiments) ..... 2. L. HYPOLEUCA
aa. Leaves glabrous or essentially so ..... 3. L. PLATYPUS

1. LICANIA ARBOREA Seem. Bot. Voy. Herald, 118, *pl. 25*. 1852–53.

Licania Seleriana Loes. Verh. Bot. Ver. Brandenb. 53:55. 1911.

Tree to 10 m. tall (or sometimes up to 30 m., according to Standley) with broad stiff blunt, oval or oblong leaves; juvenile foliage, branchlets and inflorescence conspicuously yellowed, very densely hirsutulous with short erect or somewhat matted tawny hairs; branches and upper surface of mature leaves glabrate, the lower leaf-surfaces strongly whitened with a closely felted tomentum; branchlets stout, often 3–6 mm. in diameter at the base of the inflorescence, the bark reddish-brown with inconspicuous pale lenticels. Leaf-blades coriaceous, ovate to elliptic or oblong, broadly rounded at apex, obtuse or (usually) subcordate at base, 5–12 (–15) cm. wide, 6–18 (–25) cm. long, usually 1.4–1.7 times as long as wide, lustrous and glabrous above; lateral veins about 12–15 pairs, widely divergent, the 3–5 proximal pairs much closer together than the others, all raised and forming conspicuous ribs on the lower surface; petioles stout, 5–10 mm. long, 2–3 mm. in diameter; stipules 1–1.5 cm. long, 1–2 cm. wide, linear, acute, appressed, on shoots

only. Flowers essentially sessile, very many together in axillary and terminal panicles at the tips of branches, forming an inflorescence often up to 40–50 cm. long and nearly as broad, with widely divergent branches; petals white, hirsute, oblanceolate or obovate, often about 1.5–2 mm. long and half as wide, obtusely pointed at apex, cuneate at base; stamens about 20 (the anther-bearing ones 10 or fewer), the filaments up to about 3 mm. long, hirsute, their bases coherent into a cylinder and inserted with the calyx, the sterile ones often short and inconspicuous; anthers about 0.5 mm. long; hypanthium deeply cup-shaped, about 1.5–2 mm. wide and high in anthesis, tomentose within, usually contracted toward apex and surmounted by the 5 erect or converging calyx-lobes which are triangular, acute, about 1–1.5 mm. wide and long; ovary sessile at the bottom of the hypanthium, nearly globose, about 1 mm. long, hirsute; style about 2.5 mm. long, subulate, hirsute except for the distal 0.5 mm. which is slender, terete, and glabrous; stigma terminal, slightly flattened. Fruit (said by Seemann to be black) obovoid or oblong-obovoid, 2–3 cm. long or larger, rounded at tip, substipitate, glabrate.

Western Mexico (Guerrero) to Panama, lowland, often in dry brushy forest; Colombia.

CANAL ZONE: Chiva-Chiva trail, Red Tank to Pueblo Nuevo, *Piper 5713, 5738;* old Las Cruces trail between Fort Clayton and Corozal, *Standley 29089.* COCLÉ: north rim of El Valle de Antón, *Allen 1741;* Penonomé and vicinity, *Williams 338.* CHIRIQUÍ: David, *Pittier 2841.* PANAMÁ: Sabanas, *Bro. Paul 290;* Corozal road near Panamá, *Standley 26847;* Matías Hernández, *Standley 28952;* between Matías Hernández and Juan Díaz, *Standley 32007.*

The large seed of this species is said to contain about 30 percent of oil, and to burn readily. The oil is similar to that produced commercially from the seeds of a closely related species, *Licania rigida* Benth., of Brazil. The type specimen of *Licania arborea* was collected by Seemann between Tolé and David, in what is now the Province of Chiriquí.

2. LICANIA HYPOLEUCA Benth. Bot. Voy. Sulphur, 91, *pl. 32.* 1844.

Tree 10–15 m. tall, with a trunk-diameter of 10–40 cm., the ovate or lanceolate pointed leaves whitened beneath, the branchlets slender (1–2 mm. thick at the base of the inflorescences), nearly black, glabrate (in the juvenile state densely sordid-puberulent). Leaves ovate to lanceolate or elliptic, the upper surface lustrous and glabrous but the veins and veinlets in fully mature leaves marked with lines of tiny closely set papillae, the lower surface (appearing glaucous to the unaided eye because of the fineness of the tomentose layer) whitened with a dense appressed tomentum, the main lateral veins densely puberulent or thinly tomentose, arcuate, 6–8 pairs, prominent beneath, inconspicuous above (in dried material); blades acute to acuminate at tips, acute to rounded at base, 5–12 cm. long, 2–5 cm. wide, usually about 2–2.7 times as long as wide; petioles stout, about 1 mm. in diameter and 4–7 mm. long, densely short-hairy, the hairs on the upper side extending 2–4 mm. in a narrow inverted V onto the base of the blade; stipules subulate, 1–3 mm. long, subper-

sistent, erect and parallel to the branchlets. Flowers (said to be white) very small, numerous in leafy, terminal, mostly pyramidal panicles 10–20 cm. long; lower (axillary) branches of the panicle widely divergent, often 6–15 cm. long, most of the flowers borne in racemoid arrangement along secondary branches in 2- to 5-flowered cymules on peduncles 2–5 mm. long; terminal flowers of the cymules often pedicellate 1–3 mm., the lateral ones usually nearly sessile; corolla none; anther-bearing stamens usually 3 (opposite 3 adjoining calyx-lobes), less than 1 mm. long, the filaments subulate, dilated at base and hirsute about the zone of insertion, the anthers about half as long as the filaments; hypanthium campanulate or turbinate, about 1.5–2 mm. long and wide in anthesis, often contracted slightly at mouth, surmounted by the 5 ovate-acute, entire calyx-lobes which are spreading at tips, about 1 mm. long and wide; receptacle thickly hairy within, with a prominent fringe of hairs at the somewhat thickened margin, which in addition often bears short sterile filaments alternating with the calyx-lobes, and less often bears very short vestigial filaments elsewhere; ovary sessile at the bottom of the hypanthium, ovoid-globose, less than 1 mm. long, white-hirsute; style erect (in the flower opposite the stamens and so alternating with the stamenless calyx-lobes), about 2 mm. long, subulate, hirsute except for the slender tip 0.2–0.3 mm. long; developing ovary elongating at base and becoming stipitate at maturity. Fruit pyriform, red, thinly pubescent at least at base, about 1 cm. thick and 2 cm. long (including the attenuate base).

Tabasco and British Honduras to Panama, lowland, in wet or moist forests; Colombia?

The TYPE of this species came from "Veragua", according to Bentham's original description; in Seemann's "Flora of the Isthmus of Panama", published a decade after Bentham's description, the locality was given as "Province of Veraguas", the implication being that no more definite locality could be given. At this period Veraguas included all of what is now the Province of Chiriquí, so the type-locality of this species may have been almost anywhere along the Pacific Coast of western Panama. The species is reported by Standley (Contr. U. S. Nat. Herb. 27:189. 1928) from Barro Colorado Island, with the notation that this is the only locality at which it is known to occur in the Canal Zone.

CANAL ZONE: Barro Colorado Island, *Standley 31323, 31416, 41067.* DARIÉN: La Palma, *Pittier 5491.*

3. LICANIA PLATYPUS (Hemsl.) Fritsch in Ann. K. K. Naturhist. Hofmus. Wien 4:53. 1889; Pittier in Contr. U. S. Nat. Herb. 13:443, *pl. 86.* 1912; Standl. & Steyerm. in Fieldiana Bot. 24[4]:456. 1946.

Moquilea platypus Hemsl. Diagn. Pl. 1:9. 1878; Biol. Centr.-Am. Bot. 1:366. 1880.

Tree up to 50 m. high with large, narrow, glabrous, somewhat distichous leaves; branchlets stout, glabrous, purplish or red, often 2–3 mm. in diameter at the base of the inflorescence, the lenticels numerous, narrowly elliptic, 0.5 mm. long; leaf-blades coriaceous, elliptic-lanceolate or narrowly oblong, rounded grad-

Fig. 72. *Licania platypus*

ually to a short-acuminate tip, rounded or acute at base, 3–6 (–8) cm. wide, 10–30 cm. long, usually 3 times as long as wide, green and somewhat lustrous above, paler and somewhat glaucous beneath; midvein raised and rather prominent beneath; lateral veins 12–20 (–25) pairs, arcuate, anastomosing near the margin; lower surface of the blade bearing small oval or circular glands 0.2–0.3 mm. across, these 0.2–1.5 mm. from the margin, slightly sunken, rimmed, one near the end of each main lateral vein; petioles dark red (when dry), 9–15 mm. long, 2 mm. in diameter; stipules dark, erect, stiff and persistent, 2.5 mm. long, adnate to the petiole three-fourths their length, the tip free, rounded. Flowers white, fragrant,

subsessile or on pedicels 1–2 mm. long, very many together in axillary and terminal cano-tomentose panicles at the tips of branches, these forming a divaricately branching inflorescence 10–35 cm. long; panicle branches strongly flattened near base, bractless at flowering time; petals obovate, 2–3 mm. long, finely white-tomentulose distally (often said to be ciliate); stamens 15 (–18), glabrous, subequal, the filaments up to 3 mm. long, inserted separately on the margin of the thickened disk, which is heavily retrorsely bearded; anthers about 0.5 mm. long; hypanthium cup-shaped, about 1.5 mm. high and 2 mm. wide in anthesis, tomentulose without, silky within, the erect or spreading calyx-lobes obtusely triangular with rounded sides, about 1.3 mm. long and wide; ovary sessile at the bottom of the hypanthium, nearly globose, about 1 mm. long, hirsute; style 5–6 mm. long, subulate, hirsute except for the distal one-third which is terete, filiform. Fruit (according to Pittier) very large, 1–3 to each panicle, 15–20 cm. long, 10–14 cm. in diameter, with dark brown, verrucose skin covered with white lenticels, and the inside flesh yellow, juicy, and sweet, somewhat fibrous; seed usually one, ovate-oblong, flattened, 6–8 cm. long, 4–4.5 cm. in largest diameter.

Southern Mexico to Panama; reported from Colombia. In lowland forests, often at elevations less than 400 meters, often cultivated for ornament.

PANAMÁ: along Río Juan Díaz above Juan Díaz, *Allen 941*.

This species is reported from San José Island by Johnston (Sargentia 8:132. 1949), who gives at the same time a good descriptive account of the tree as it occurs in the forest on the island.

The native country of this tree is somewhat in doubt; Pittier remarks that he has never seen it in a truly wild state. Hemsley's original material included a cultivated specimen from Nicaragua (designated as the type-specimen in Contr. U. S. Nat. Herb. 23:344. 1922), and Cuming's *No. 1272*, originally supposed to have come from Panama (i. e. probably western Panama). As Hemsley later pointed out (Biol. Centr.-Am. Bot. 1:366. 1880), "Cuming's specimens may have been collected further south, in Western Colombia." (i. e. probably what is now eastern Panama).

9. HIRTELLA L.

HIRTELLA L. Gen. Pl. ed. 5, 20. 1754; Hook. f. in Mart. Fl. Bras. 14^2:27–40. 1867; Standl. & Steyerm., in Fieldiana, Bot. 24^4:450–452. 1946.

Shrubs or trees with alternate, simple, entire leaves. Flowers in axillary and terminal panicles or racemes; hypanthium short and symmetrical or elongated and then usually gibbous, the lobes 5, reflexed; petals 5; stamens 3–7 (rarely more), inserted at the summit of the hypanthium disk, usually unilaterally inserted (i. e. on the side where the ovary is attached, opposite the style and the enlarged side of the hypanthium); ovary unilocular, hirsute, attached to the side of the hypanthium-tube above the base (i. e. below the base of the middle stamen); style basal. Fruit drupaceous, often dry.

a. Inflorescence racemoid, the 30–40 flowers on unbranched filiform bracteolate pedicels 5–8 (–12) mm. long; stamens 5–7 ..... 2. H. RACEMOSA
aa. Inflorescence a leafless spike-like panicle, the lateral branches (cymes) often 1.5 cm. long, the spikes sometimes appearing racemoid when most of the cymes are reduced to 2 or even 1 flower each; stamens 3.
b. Leaves glabrate or the principal veins with persistent appressed yellowish hairs; bracts of the cymes lanceolate, attenuate, minutely glandular-denticulate ..... 3. H. TRIANDRA
bb. Leaves sparsely or densely short-hirsute, at least on the veins, with erect rufous or tawny hairs; bracts of the cymes round or oval, heavily beset with depressed or stalked and peltate glands 0.3–1 mm. across ..... 1. H. AMERICANA

1. HIRTELLA AMERICANA L. Sp. Pl. 34. 1753; Standl. & Steyerm. in Fieldiana, Bot. 24:450. 1946.

Hirtella mollicoma HBK. Nov. Gen. & Sp. 7:263. 1825; Hemsl. in Biol. Centr.-Am. Bot. 1:366. 1880, as *mollissima;* Standl. in Contr. U. S. Nat. Herb. 27:188. 1928.
?Hirtella glandulosa Spreng. Anleit., *pl. 7, f. 1–4;* Neue. Entd. 1:303. 1820; DC. Prodr. 2:528. 1825; Seem. Bot. Voy. Herald, 118. 1852–53.
Hirtella guatemalensis Standl. in Trop. Woods 11:19. 1927.

Small or medium-sized tree, the branchlets and inflorescences conspicuously rufous, densely short-hirsute with straight, slender, multicellular tawny hairs 0.5–0.7 mm. long; branchlets 2–4 mm. in diameter below the inflorescence, the hairs persistent. Leaves hairy like the stems but less densely, the upper surface glabrate in age except the midrib, the lower surface densely hairy on the principal veins and uniformly but sparsely so on the anastomosing veinlets, where the hairs are often about 3 times as long as the distance between them; hairs of the leaves with enlarged papillose bases; leaf-blades thick and subcoriaceous, oblong or elliptic, acute and gradually short-acuminate at apex, rather abruptly rounded or obtuse at base, 3–6 cm. wide, 6–15 cm. long, often 2–2.7 times as long as wide; lateral veins 8–12 pairs, arcuate, slightly impressed above, raised beneath, the small veinlets finely reticulate and often raised on the upper surface, making it rough to the touch; glands abundant on the lower surface, usually concentrated near base and apex of the blade, elliptic or circular, 0.2–0.5 mm. across, with raised rim and depressed center; petioles very stout, 2–4 mm. long and about 2 mm. thick, their surfaces concealed by the hairs; stipules subpersistent, hirsute, subulate, appressed, 6–9 mm. long. Flowers many, white or purplish-white, in very narrow spike-like leafless panicles 10–20 cm. long and 2–4 cm. thick, the lateral branches of the spike often about 1.5 cm. long, ascending, cymosely 1- or few-flowered; bracts of the cymes round or oval, 1–1.5 mm. long, heavily beset with large glands, these varying from depressed spots 0.3 mm. across to peltate glands 1 mm. across on stalks 1 mm. long, the larger glands often very numerous and conspicuous in the spikes after the abortion of most of the flowers; bracts subtending the lateral cymes (i. e. those of the main axis) eglandular or nearly so, hirsute, subulate, about 5 mm. long; petals white, broadly elliptic, bluntly rounded at base and apex, glabrous, about 4 mm. long and 3 mm. wide; stamens 3, opposite adjoining sepals, much exserted and curled into the flower, purplish or deep red, glabrous, the fila-

ments 1–1.2 cm. long, fleshy at base and tapering to the very slender tips, arising separately from the hypanthium-rim which is fleshy and projects about 1 mm. or a little less above the base of the calyx; anthers about 0.6 mm. long; hypanthium turbinate, the cavity funnelform, about 2 mm. deep measured from the summit of the fleshy rim, retrorsely hairy within the rim but glabrous at bottom; calyx-lobes broadly oblong, obtuse to rounded at tips, reflexed at and after anthesis, entire, 1.5–2.2 mm. wide, 2–2.7 mm. long, the outer surface thinly yellow-hirsute like the inflorescence, the inner surface pale, sordid-tomentulose; ovary hairy, sessile, attached above the middle of the hypanthium cavity (at the base of the middle stamen), the style about as long as the stamens and opposite them in the flower, filiform, long-pilose below the middle, with tiny capitate stigma, in bud bent abruptly away from the ovary and then coiled toward it. Fruit oval, thinly yellow-hairy, rounded at apex, probably 1–1.5 cm. long or longer, black.

Cuba; British Honduras, Costa Rica, and Panama; Colombia and northern Venezuela; thickets and savannas, lowlands.

A distinct entity, but probably the same species, occurs in Guatemala and southern Mexico; the pubescence in general is toward yellowish rather than reddish, the calyx-lobes are sordid-tomentulose and pale on the outer surface as well as the inner, and the glands are usually absent from the lower leaf-surfaces but are usually present on the upper.

CANAL ZONE: Gatuncillo, *Piper 5654;* between Río Grande and Pedro Vidal, road to Arraiján, *Pittier 2708;* [Cruces, *Seemann*]; southwest of Pt. Salud, Barro Colorado Island, *Woodworth & Vestal 728.* COCLÉ: Penonomé, *Williams 247.* PANAMÁ: Chorrera, *Killip 3409;* Pacora, *Bro. Paul 284;* Sabanas, north of Panamá, *Bro. Paul 412;* San José Island, *Erlanson 108.*

2. HIRTELLA RACEMOSA Lam. Encycl. Meth. 3:133. 1789; DC. Prodr. 2:529. 1825; Seem. in Bot. Voy. Herald, 119. 1852–53; Standl. & Steyerm. in Fieldiana, Bot. 24:450–452. 1946.

Hirtella americana Aubl. Hist. Pl. Guian. Fr. 247, *pl. 98.* 1775; Hook. f. in Mart. Fl. Bras. 14[2]:33. 1867; Benth. in Bot. Voy. Sulphur, 91. 1844; Standl. in Contr. U. S. Nat. Herb. 27:188. 1928; auct. Amer. plur., non L.
Hirtella oblongifolia DC. Prodr. 2:529. 1825.

Shrub or small tree, 2–3 (–6) m. tall, with slender pubescent branchlets 1–1.5 mm. in diameter below the inflorescence; hairs of two types, those of the young foliage and branchlets yellowish, appressed or erect, straight and slender, pointed, multicellular, 0.5–1.5 mm. long, these also abundant in the inflorescence but there mixed with tiny erect white hairs mostly 0.2–0.3 mm. long. Leaves elliptic to oblong, lanceolate, or ovate, glabrate, only a few long yellow hairs persistent on the veins (at least of the lower surface), a few of the hairs with papillose bases; blades subcoriaceous, lustrous, 1.5–4 cm. wide, 3–8 cm. long, usually 2–3 times as long as wide, narrowed from the middle or above to a broad blunt or pointed acumen 1 cm. long or less, narrowed and rounded at base (or obtusely narrowed, with the extreme base rounded abruptly into the petiole); petiole short, stout, about 0.7

mm. in diameter, 2 mm. long; lateral veins 6–8 pairs, arcuate, slightly raised on both surfaces but not forming conspicuous ribs on either, often hardly visible on the upper; glands occurring on the lower surface of the blade near base, mostly nearly circular, about 0.2 mm. across, with raised rim and depressed center; stipules subpersistent, filiform-subulate, appressed-hairy, 2.5–5 mm. long, usually black in dried material, appressed to the branchlets. Flowers in axillary and terminal racemes 12–15 cm. long (or up to 20–25 cm. including the basal leafy part of the growing branchlet terminated by the raceme); "racemes" 30- to 40-flowered, flowering from base to apex but apparently always determinate, the terminal (bractless) flower abortive; lateral flowers on filiform "pedicels" 5–8 (–12) mm. long, spreading at right angles or somewhat ascending, each with two tiny bracteoles near base or about one-third the distance from base to apex, the bracteoles often with sessile or stalked glands on the margins, and borne at the summit of a thickened peduncular portion of the flower-stalk (only the part beyond them being the pedicel proper); bracts subtending the flower-stalks lanceolate, usually recurved, 1–2 mm. long, with basal marginal glands like those of the leaves (and sometimes a similar gland at apex); petals pink, purple or "rosy mauve", glabrous, broadly elliptic, rounded at both ends, 2–3 mm. wide, 3–5 mm. long; stamens 5–7, much exserted, purple, glabrous, the filaments 1.2–1.6 cm. long, fleshy at base and tapering to the very slender tips, arising separately from the fleshy hypanthium-rim which projects 1 mm. or less above the base of the calyx, absent from the segment of the rim opposite the insertion of the ovary or there represented by vestigial staminodia only; anthers about 0.6 mm. long; hypanthium in anthesis elongate-tubular, with hollow cylindric or oblong one-sided base up to about 1 mm. thick and 2 mm. long, and funnelform throat about 1 mm. long, the interior hairy about the summit of the throat, glabrous below; calyx-lobes oblong or elliptic, usually reflexed at anthesis, entire, rounded or subacute at apex, about 1–1.5 mm. wide, 2.5 mm. long, the outer surface with mixed short white and long yellow hairs, the inner surface glabrous proximally, distally white-tomentulose; ovary hirsute, sessile, attached to one side of the funnelform portion of the hypanthium above the bottom; style as in *H. americana*, but up to about 1.5 cm. long, arising from the flower toward the side where functional stamens are lacking (i. e. the side toward which the inflated base of the hypanthium is expanded). Fruit oblong-obovoid, sparsely hairy, dark red or purple, up to about 1.5 cm. long and 0.6 cm. in diameter, rounded at apex, the base substipitate.

Guerrero and British Honduras to Panama, northern South America, and south in the Amazon Basin to central Brazil, eastern Peru and eastern Bolivia; lowlands, in forests and thickets.

CANAL ZONE: Summit Road, *D. G. Jones 277;* Ancón Hill, *Piper 5575, 5596; Pittier 2075;* between Miraflores and Corozal, *Pittier 2192;* between Corozal and Ancón, *Pittier 2641;* road to Arraiján, between Río Grande and Pedro Vidal, *Pittier 2702;* Ancón Hill, *Standley 26366;* Corozal, *Standley 27371;* Gamboa, *Standley 28370;* Summit, *Standley 30107;* Obispo, *Standley 31742;* Río Chagres, *Steyermark & Allen 17500;* Barro Colorado Island, *Wetmore & Abbe 105; Woodworth & Vestal 332.* COCLÉ: Penonomé, *R. S.*

Williams 91. COLÓN: vicinity of Santa Rosa, Río Gatuncillo, *Allen 4156.* DARIÉN: La Palma, *Pittier 5486.* PANAMÁ: Río Las Lajas, *Allen 1603;* Las Sabanas, *Killip 3361; Macbride 2645;* La Chorrera, *Bro. Maurice 816;* Isla Taboga, *Miller 2035; Standley 27036, 28017;* Tumba Muerto road near Panamá, *Standley 29736.* PROVINCE UNKNOWN: "Panama", *Duchassaing* in 1850.

According to Johnston (Sargentia 8:131–132. 1949), the true *Hirtella racemosa* is a South American species with larger flowers than the Panamanian and Central American species, which he refers to *H. oblongifolia* DC. Under the name of *H. oblongifolia,* he reports the species as a very common shrub on San José Island.

3. HIRTELLA TRIANDRA Sw. Prodr. Veg. Ind. Occ. 51. 1788.

Large shrub or a tree, often 5–6 m. high (sometimes to 20 m. with a trunk 15–20 cm. in diameter), with slender pubescent branchlets 1–2 mm. in diameter below the inflorescences; inflorescences and juvenile foliage and branchlets more or less appressed-pubescent with two types of hairs intermingled: straight, slender, pointed, yellow or tawny, usually appressed hairs 0.5–1 mm. long, and straight or crisped often erect white hairs 0.3 mm. long or less; the longer, yellow hairs predominating on the leaves, while in the inflorescence the two types are often equally intermingled except on the inner surfaces of the calyx-lobes, where the shorter, white hairs alone occur. Leaves elliptic or sometimes oblong, glabrate or the principal veins persistently hairy, the hairs of the leaves often with enlarged papillose bases; blades rather thin, 2–5 cm. wide, 6–12 (–15) cm. long, 2–3 times

Fig. 73. *Hirtella triandra*

as long as wide, rather abruptly acute at apex and with a definite narrow sharp-pointed acumen 0.6–2 cm. long; base of blades acutely narrowed from below the middle, the extreme base not decurrent but often abruptly rounded and so truncate or even subcordate, and sharply delimited from the stout petiole 1–2 mm. thick and 2–4 mm. long; lateral veins 5–8 pairs, arcuate, not very prominent, slightly elevated on the lower surface; glands occurring on the lower surface of the blade (occasionally on the upper surface), mostly near base, often very small, 0.2 mm. across, but sometimes reaching 0.5 mm., elliptic or circular, with raised rim and depressed center; stipules subpersistent, hirsute, subulate, appressed, 3–5 mm. long. Flowers in axillary and terminal raceme-like panicles 3–7 cm. long, the "racemes" compound but the lateral cymes most often reduced each to 1 or 2 flowers and the inflorescence giving the appearance of a simple raceme with bracteolate pedicels 8–15 mm. long (actual pedicels 2–3 mm. long); bracts of the cymes lanceolate, attenuate, minutely glandular-denticulate, 1.5–3 mm.; petals white, broadly elliptic, rounded at both ends, about 5 mm. long and 3–3.5 mm. wide, glabrous; stamens 3, opposite adjoining sepals, much exserted, pink or purple, glabrous, the filaments 1.2–1.6 cm. long, fleshy and about 1 mm. wide at base and tapering to the very slender tips, arising separately from the hypanthium-rim which is fleshy and projects about 0.5 mm. above the base of the calyx; anthers about 0.6 mm. long; hypanthium campanulate, the cavity funnelform, about 1.8–2 mm. deep, retrorsely hairy within the fleshy rim but glabrous at bottom; calyx-lobes oblong to suborbicular, rounded at tips, reflexed after anthesis, entire, 2–2.5 mm. wide, 3–3.5 mm. long, the outer surface with long yellow appressed hairs and scattered small white hairs also, the inner surface white-tomentulose; ovary hirsute, sessile; style as in *H. americana,* but up to 1.5 cm. long. Fruit dark red or purple, oblong-obovoid, up to 2.3 cm. long and 15 mm. thick, with rounded apex and thick, short, stipe-like base, rather densely yellow-hairy.

West Indies; British Honduras and Guatemala to Panama; northern South America and south in the Amazon basin to southern Brazil, eastern Peru and eastern Bolivia; low and middle elevations, in moist or wet forests.

BOCAS DEL TORO: Fish Creek hills, *von Wedel 2457.* CANAL ZONE: Barro Colorado Island, *Bangham 398; Salvoza 865; Wetmore & Abbe 198; Woodworth & Vestal 647;* Frijoles, *Pittier 2680;* along Río Indio de Gatún, *Pittier 2784;* Fort Sherman, *Standley 31135.* COLÓN: along Río Fató, *Pittier 3869;* Santa Isabel, *Pittier 4178.* DARIÉN: El Real, *Allen 967;* Garachiné, *Pittier 5523;* Pinogana, *Pittier 6577;* Cituro, *R. S. Williams 667.* PANAMÁ: hills above Campana, *Allen 1689;* Pacora, *Allen 3453;* near Vigía and San Juan on Río Pequení, *Dodge, Steyermark & Allen 16524;* near Chepo, *Kluge 48;* Río Tataré, *Woodson & Schery 1008.* ?SAN BLAS: Permé, *Cooper 286;* Marraganti [?Mazargandi], *R. S. Williams 1000.*

10. COUEPIA Aublet

COUEPIA Aubl. Hist. Pl. Guian. Fr. 519, *pl. 207.* 1775; Hook. f. in Mart. Fl. Bras. 14^2:40–49. 1867.

Trees or shrubs, with alternate, simple, entire leaves. Flowers in racemes or panicles; hypanthium elongate and somewhat tubular, often gibbous at the base,

the lobes 5; petals usually 5; stamens 10–15 or numerous, inserted at the summit of the hypanthium tube, the filaments more or less united at base in a complete or incomplete ring; ovary unilocular, hairy, attached to the side of the hypanthium-tube above the base. Fruit a dry or fleshy drupe, the stone mostly woody, 1-seeded.

1. Couepia panamensis Standl. in Trop. Woods 42:22. 1935.

Tree up to 20 m. tall, nearly glabrous, the petioles, young growth, and inflorescence sparsely strigose with appressed sordid hairs 0.5 mm. long or less, the inner calyx-lobes canescent-puberulent near tips; branchlets dark reddish brown, glabrescent, about 2 mm. thick below the inflorescence, the lenticels inconspicuous. Leaves ovate or elliptic, the tip acute and terminated by a blunt acumen about 1–1.3 cm. long and 2–4 mm. wide, the base of the blade acute and attenuate into a stout petiole 1.5–2 mm. thick and 4–6 mm. long; petiolar glands elliptic, near summit of petiole, about 1.5–1.8 mm. long, with raised margin and a flat sunken central area; similar but much smaller glands (about 0.5 mm. long) occur at intervals along the margins of the blades, especially near tips; blades 3–5 cm. wide, 8–12 cm. long, 2–2.5 times as long as wide, lustrous on both surfaces when dry, the veins inconspicuous, arcuate, about 5–6 pairs, those near apex usually anastomosing and not forming well-marked ribs; stipules not seen. Flowers "greenish to pale white", in small terminal panicle-like clusters 6–8 cm. long; petals fleshy, glabrous, strongly concave (at least in bud; open flowers not seen), broadly elliptic, rounded at apex and base, about 4 mm. wide and 5 mm. long; stamens about 20, mostly antheriferous, the filaments glabrous, about 6 mm. long in bud, their bases coherent into an incomplete ring, the anthers about 1 mm. wide and long; hypanthium long-campanulate, in bud about 3 mm. in diameter and 5–6 mm. long, attenuate to a pedicel 5–8 mm. long, enlarged at apex into the 5 fleshy and strongly imbricate suborbicular entire calyx-lobes which are about 4 mm. long; receptacle funnelform and densely woolly within, the cavity 2–3 mm. deep, the basal half of the hypanthium lignified, the hirsute ovary 1 mm. or less above the bottom of the cavity; style about 3 mm. long in bud, the stigma white, peltate, flattened, about 1 mm. across. Fruit not seen.

San Blas: Permé, *Cooper 279*.

CONNARACEAE

Trees, shrubs, or woody lianas. Leaves alternate, imparipinnate, rarely unifoliolate, exstipulate; leaflets entire. Inflorescence paniculate, terminal or lateral. Flowers relatively small, regular, perfect or rarely dioecious; sepals 5, imbricate to valvate, free or rarely connate at the base, sometimes accrescent in fruit *(Rourea)*; petals 5, free or connate at the base; stamens 10, the filaments united toward the base and in alternate cycles of two lengths, the longer opposite the sepals, the shorter (sometimes staminodial) opposite the petals; carpels free, 5–1, but usually

producing a single fruit, the ovules 2 in each carpel, collateral, erect, anatropous, basal or sub-basal. Fruit a follicle, sometimes indehiscent, or a legume, containing usually a single arillate seed.

a. Carpels 5; follicles sessile.
  b. Sepals valvate, not enlarged in fruit; follicles densely ferruginous-tomentose; leaves densely and persistently pubescent ..... 1. CNESTIDIUM
  bb. Sepals imbricate, enlarged in fruit; follicles and leaves glabrous or glabrate ..... 2. ROUREA
aa. Carpels 1; follicles stipitate, essentially glabrous; leaves glabrous or glabrate ..... 3. CONNARUS

1. CNESTIDIUM Planch.

CNESTIDIUM Planch. in Linnaea 23:439. 1850; Schellenb. in Engl. Pflanzenreich IV. 127 (Heft 103):191. 1938.

Woody lianas. Leaves imparipinnate. Inflorescence paniculate, pseudoterminal in the axils of the upper leaves. Flowers small, eglandular, subsessile; sepals valvate, not enlarged in fruit; carpels 5. Follicles almost always solitary, sessile, very densely ferruginous-tomentose without, containing a single arillate seed.

In addition to the following species, one other occurs in the Guianas.

1. CNESTIDIUM RUFESCENS Planch. in Linnaea 23:440. 1850.

Rourea frutescens Aubl. ex Griseb. in Bonplandia 6:6. 1858.
Rourea hondurensis Donn. Sm. in Bot. Gaz. 40:2. 1905.

Woody lianas as much as 12 m. high, sometimes attaining the proportions of a slender tree. Leaves large, with 7–9 oblong to obovate-oblong leaflets 3–9 cm. long which are persistently ferruginous-pubescent, particularly beneath. Flowers subsessile, numerous, in densely ferruginous-pubescent, pseudoterminal panicles 10–15 cm. long; sepals about 3 mm. long; petals white, very slightly longer than the sepals. Follicles sessile, densely ferruginous-tomentose, 1.0–1.5 cm. long, 5–7 mm. broad.

Moist or swampy forests and thickets from sea-level to about 120 m.; common in most of Panama; southern Mexico to Colombia; Cuba.

CANAL ZONE: Barro Colorado Island, *Shattuck 1038, 1127; M. Brown 96, 121; Starry 137; Woodworth & Vestal 399; Van Tyne s. n.; Standley 41000; Bangham 403;* drowned forest near Vigía and San Juan, on Río Pequení, alt. 66 m., *Steyermark & Allen 16572;* vicinity of Miraflores Lake, *G. White 167;* near Cruces, *Hayes 936;* Frijoles, *Piper 5834; Allen 925;* near Fort Randolph, *Standley 28679;* along old Las Cruces Trail between Fort Clayton and Corozal, *Standley 29028, 29139;* near Summit, *Standley 29592, 30090;* vicinity of Fort Sherman, *Standley 31087;* Obispo, *Standley 31744;* Gamboa, *Stevens 1111;* between France Field, C. Z., and Cativa1, Province of Colón, *Standley 30172.* CHIRIQUÍ: vicinity of San Felix, alt. 0–120 m., *Pittier 5740.* COCLÉ: between Aguadulce and the Chico River, *Pittier 5104;* Penonomé and vicinity, *Williams 186.* BOCAS DEL TORO: Water Valley, *von Wedel 895.* PANAMÁ: Punta Paitilla, *Piper 5429;* between Pacora and Chepo, *Woodson, Allen & Seibert 1645;* Camino del Boticario, near Chepo, *Pittier 4553;* near Matías Hernández, *Standley 28953;* Río Tecúmen, *Standley 29432, 29443;* Cerro Campana, *Allen 2681;* Tumba Muerto Road near Panamá, *Standley 29741;* San José Island, *Erlanson 560;* Taboga Island, *Barclay s. n.; G. S. Miller 1842; Standley 27985.*

2. ROUREA Aublet

ROUREA Aubl. Hist. Pl. Guian. Fr. 1:467. 1775; Schellenb. in Engl. Pflanzenreich IV. 127 (Heft 103):194. 1938.

Robergia Schreber, Gen. 1:309. 1789.
Malbrancia Necker, Elem. Bot. 2:366. 1790.
Eichleria Progel, in Mart. Fl. Bras. 12^2:518. 1877.

Woody lianas, sometimes nearly erect shrubs or trees. Leaves imparipinnate, rarely unifoliolate, when pinnate the lateral leaflets usually approximate or alternate rather than strictly opposite. Inflorescence terminal, pseudoterminal, or lateral, paniculate, usually more slender and with fewer flowers than in the two other genera. Flowers small, usually distinctly pedicellate; sepals imbricate, conspicuously enlarged in fruit, sometimes glandular; carpels 5. Follicles almost always solitary, sessile, glabrous or essentially so, containing a single arillate seed.

A genus of the American tropics containing about 32 species according to Schellenberg. The plants normally are woody lianas, but in the absence of suitable support may become erect or nearly so.

a. Calyx glandular, tomentose.
  b. Flowers yellowish green; sepals 3–4 mm. long; leaflets 6–17 cm. long, densely tomentulose beneath ..... 1. R. PITTIERI
  bb. Flowers white; sepals 1.5–2.0 mm. long; leaflets 3–10 cm. long, very inconspicuously puberulent to glabrate beneath ..... 2. R. ADENOPHORA
aa. Calyx eglandular, glabrous or inconspicuously ciliolate; leaflets 4–12 cm. long, glabrous ..... 3. R. GLABRA

1. ROUREA PITTIERI S. F. Blake, in Bull. Torrey Bot. Club 50:274. 1923.

Woody lianas. Leaves imparipinnate, leaflets 5–7, broadly elliptic, apex subcaudate-acuminate, rarely obtuse, 6–17 cm. long, 3.5–8.5 cm. broad, glabrous above, densely tomentulose beneath. Sepals 3.5–4.0 mm. long in flower, 4.5–5.0 mm. in fruit, glandular and densely tomentulose without; petals yellowish green, 4–5 mm. long. Follicles about 1.5 cm. long, glabrous.

Panama, in moist thickets and forests, ascending to about 700 m. altitude.

COLÓN: Loma de la Gloria, near Fató (Nombre de Dios), *Pittier 4247*. DARIÉN: foothills of Garagará, Sambú basin, *Pittier 5613*; Cana-Cuasi Trail, Chepigana Distr., *Terry & Terry 1536*.

2. ROUREA ADENOPHORA S. F. Blake, in Bull. Torrey Bot. Club 50:273. 1923.

Woody lianas. Leaves imparipinnate, leaflets 3–7, rarely 1, broadly oval to rather narrowly oblong-elliptic, apex narrowly subcaudate-acuminate, rarely obtuse, 3–10 cm. long, 1.5–5.0 cm. broad, glabrous above, very inconspicuously puberulent to glabrate beneath. Sepals 1.5–2.0 mm. long in flower, 3.5–4.0 mm. in fruit, glandular and finely pilosulose without; petals white, about as long as the sepals. Follicles about 1.5 cm. long, glabrous or glabrate.

Panama, in moist thickets and forests at altitudes near sea-level.

CANAL ZONE: vicinity of Frijoles, *Piper 5812*; near mouth of Río Chagres, *Allen 887*; vicinity of Summit, *Standley 30102*; between Gatún and Lion Hill, *Pittier 2566*; near Old

Fort Lorenzo, mouth of Río Chagres, *Piper 5976;* Santa Rita Trail, *Cowell 111;* Barro Colorado Island, *Standley 40971; Bangham 487;* hills west of Canal, near Gatún, *Standley 27216.* CHIRIQUÍ: forests around Puerto Remédios, *Pittier 3380.*

3. ROUREA GLABRA HBK. Nov. Gen. & Sp. 7:41. 1825.

Connarus glaber DC. Mem. Soc. Hist. Nat. Paris 2:385. 1825.
Robergia glabra (HBK.) Spreng. Syst. 4^2:188. 1827.
Rourea oblongifolia Hook. & Arn. Bot. Beechey Voy. 283. 1836.
Santalodes glabrum (HBK.) O. Ktze. Rev. Gen. Pl. 1:155. 1891.

Fig. 74. *Rourea glabra*

Woody lianas. Leaves imparipinnate, leaflets 3–5, elliptic to oval, apex subcaudate-acuminate to obtuse, 4–12 cm. long, 2–6 cm. broad, glabrous. Sepals 2–3 mm. long in flower, 4–5 mm. in fruit, eglandular, glabrous or inconspicuously ciliolate; petals white, 5–6 mm. long. Follicles about 1.5 cm. long, glabrous.

Southern Mexico to southern Brazil; Cuba and Jamaica. In Panama a frequent liana in moist thickets and forests at lower elevations.

CANAL ZONE: near Fort Randolph, *Standley 28686;* Gamboa, *Stevens 1094;* Ancón Hill, *Standley 26381;* Chagres, *Fendler 57;* vicinity of Salamanca Hydrographic Station, Río Pequení, *Woodson, Allen & Seibert 1556;* between France Field, C. Z., and Catival, Province of Colón, *Standley 30180.* COCLÉ: Penonomé and vicinity, *Williams 140.* PANAMÁ: between Matías Hernández and Juan Díaz, *Standley 32016;* near the big swamp east of the Río Tecúmen, *Standley 26703;* Paitilla, *Bro. Heriberto 208;* Isla Taboga, *Woodson, Allen & Seibert 1533.*

3. CONNARUS L.

CONNARUS L. Sp. Pl. 2:675. 1753; Schellenb. in Engl. Pflanzenreich IV. 127. (Heft 103):216. 1938.

Omphalobium Gaertn. Fruct. 1:217. 1788.
Thysanus Lour. Fl. Cochinch. 1:284. 1790.
Canicidia Vell. Fl. Flum. 4:*pl. 139.* 1827.
Erythrostigma Hassk. in Flora 25:Beibl. 2:45. 1842.
Anisostemon Turcz. in Bull. Soc. Nat. Mosc. 2:152. 1842.
Tricholobus Bl. Mus. Bot. Lugd. Bat. 1:236. 1850.

Woody lianas, shrubs, or trees. Leaves imparipinnate, rarely unifoliolate. Inflorescence paniculate, terminal and lateral in the upper leaf axils. Flowers small, glandular; sepals imbricate to subvalvate, more or less conspicuously punctate-glandular, not enlarged in fruit; petals glandular or eglandular; stamens 10, or the inner whorl reduced to staminodia, the filament and connective bearing small, sessile or stipitate glands; carpels 1. Fruit a stipitate, gibbous follicle containing a single arillate seed.

About 121 species of the tropics of both hemispheres, according to Schellenberg. In Panama the species are woody lianas, occasionally erect or suberect, inhabiting moist forests and thickets at low elevations.

a. Inflorescence densely and persistently ferruginous-tomentulose, the flowers sessile or subsessile; leaflets usually 3, 6–20 cm. long ..... 1. C. PANAMENSIS
aa. Inflorescence inconspicuously pilosulose to glabrate, the flowers shortly but definitely pedicellate.
  b. Leaflets usually 5, broadly oval to oblong-elliptic, broadly obtuse to rounded at the base, 3–12 cm. long ..... 2. C. TURCZANINOWII
  bb. Leaflets usually 3, oblanceolate, rather narrowly cuneate at the base, 10–25 cm. long ..... 3. C. WILLIAMSII

1. CONNARUS PANAMENSIS Griseb. in Bonplandia 6:6. 1858, non Turcz.

Connarus haemorrhoeus Karst. Fl. Columb. 2:73. 1866–69.
Connarus Cooksii Pittier, ex Schellenb. in Engl. Pflanzenreich IV. 127. (Heft 103):223. 1938, nom. nud. in synon.

Woody lianas, sometimes erect or suberect. Leaflets usually 3, rarely 5, elliptic to oval, broadly obtuse at the base, 6–20 cm. long, 2–10 cm. broad on flowering or

fruiting branches, sometimes larger on vegetative stems, ferruginous-tomentulose to glabrate. Inflorescence densely and persistently ferruginous-tomentulose, spicate-paniculate, the small yellowish flowers sessile or subsessile. Sepals ovate, about 1.5 mm. long; petals about 2.5 mm. long. Follicles obliquely compressed-obovoid, about 1.5 cm. long and 1 cm. broad, with a stipe about 3–4 mm. long.

Costa Rica to Colombia.

CANAL ZONE: Barro Colorado Island, *Standley 31425; Woodworth & Vestal 426; Starry 207; Bailey 224; Bangham 399, 418; Aviles 10;* Cerro Gordo, near Culebra, *Pittier 2314;* Río Agua Salúd, near Frijoles, *Piper 5862;* vicinity of Pacora, *Allen 1008;* along Río Tecúmen, north of Chepo Road, *Hunter & Allen 230;* Río Tapía, *Standley 28212;* Isla Taboga, *Woodson, Allen & Seibert 1449;* San José Island, *Erlanson 85.* CHIRIQUÍ: Remédios and vicinity, *Pittier 5470.* COCLÉ: Penonomé and vicinity, *Williams 376;* between Paso del Arado and Olá, *Pittier 5010.*

2. CONNARUS TURCZANINOWII Triana, in Ann. Sci. Nat. V. 16:364. 1872.

Connarus panamensis Turcz. in Bull. Soc. Nat. Mosc. 22:277. 1859, non Griseb.

Woody lianas, sometimes becoming erect or suberect. Leaflets usually 5, broadly oval to oblong-elliptic, broadly obtuse or rounded at the base, 3–12 cm. long, 1.5–5.0 cm. broad on flowering or fruiting branches, glabrate or glabrous. Inflorescence inconspicuously pilosulose to glabrate, the small greenish white or yellowish flowers shortly but definitely pedicellate; sepals narrowly lanceolate, 2.0–2.5 mm. long; petals about 5 mm. long. Follicles obliquely compressed-obovoid, about 1.5 cm. long and 1 cm. broad, with a stipe about 2–3 mm. long.

Apparently endemic to Panama.

CANAL ZONE: Chagres, *Fendler 128;* Gatún, *Hayes 166, 545;* vicinity of Frijoles, *Piper 5797, 5832;* near Fort Randolph, *Standley 28603;* Barro Colorado Island, *Bailey & Bailey 322;* between France Field, C. Z., and Catival, Province of Colón, *Standley 30273.* COLÓN: Aspinwall [Colón], *Hayes 633, 639.*

It is noteworthy, perhaps, that the cited specimens of *C. Turczaninowii* are all from the Atlantic slopes of the isthmus, while those of *C. panamensis* are from the Pacific slope, with the exception of the plants from Barro Colorado Island.

3. CONNARUS WILLIAMSII Britton, in N. Am. Fl. 22^6:560. 1918.

Connarus Allenii Steyermark, in Ann. Mo. Bot. Gard. 28:430. 1941.

Woody lianas, sometimes erect or suberect. Leaflets usually 3, sometimes 5, oblanceolate, rather narrowly cuneate at the base, 10–25 cm. long, 2–8 cm. broad on fruiting branches, glabrous or glabrate. Inflorescence rather inconspicuously pilosulose to glabrate, the small flowers shortly but distinctly pedicellate; sepals 2–3 mm. long; petals 4.0–4.5 mm. long. Follicles obliquely compressed-obovoid, about 1.5 cm. long and 1.3 cm. broad, with a stipe 3–4 mm. long.

Apparently endemic to Panama.

DARIÉN: Marragantí and vicinity, *Williams 1006;* trail between Pinogana and Yavisa, *Allen 249.*

LEGUMINOSAE

Herbs, vines, shrubs or trees of exceedingly diverse habit and habitat, frequently armed (most frequently in the subfamily MIMOSOIDEAE). Leaves alternate, trifoliolate, pinnate or bipinnate or rarely simple, usually large, sometimes sensitive (folding at night or upon disturbance); petiole and rachis prominent or infrequently nearly obsolete, typically pulvinate basally, usually sulcate on the upper side and often (MIMOSOIDEAE particularly) bearing one or more glands; leaflets many or few, as a rule small, almost invariably with the margins entire, commonly oblique basally, pubescent or glabrous, the venation prominent or obscure; stipules and usually stipels present. Inflorescence axillary or terminal, indeterminate, the flowers solitary or more commonly in racemes, panicles, spikes or heads; floral bracts usually present but inconspicuous. Flowers typically, but not always, perfect, complete and 5-merous, regular, sympetalous and valvate (the great majority of the MIMOSOIDEAE) or more commonly irregular, polypetalous and imbricate (CAESALPINOIDEAE and PAPILIONOIDEAE); calyx usually synsepalous and campanulate, sometimes of separate sepals, frequently pubescent; corolla funnelform (most MIMOSOIDEAE), slightly irregular and with the upper petal to the inside (CAESALPINOIDEAE), or papilionaceous (strongly irregular with the upper standard outside the wings and keel: PAPILIONOIDEAE); stamens usually 10 (most PAPILIONOIDEAE) to many (most MIMOSOIDEAE), sometimes few (some CAESALPINOIDEAE), except in the CAESALPINOIDEAE and a few genera of other subfamilies the filaments united below; anthers bilocular, small or large, sometimes gland-bearing, in a few genera dehiscing by terminal pores; ovary unicarpellate and 1-celled, bearing 1 to many ovules from the dorsal suture, usually oblong and compressed, stipitate or sessile, surmounted by a prominent, simple style and usually a small stigma. Fruit a legume, but this extremely variable in size and shape, dehiscent or in a number of cases indehiscent, the seeds typically exalbuminous and bean-like.

The Leguminosae is an exceedingly large and diverse family, well represented in both the tropics and temperate regions (MIMOSOIDEAE and CAESALPINOIDEAE largely tropical). In spite of its inordinate size and perhaps consequent diversity, the family is quite "natural" and is seldom confused with other families. Some exceptions can be found to almost any defining characteristic, but most useful are the usually compound, alternate, stipulate leaves, flower form, and unicarpellate ovary with dorsally affixed ovules becoming in fruit a legume. The floral differences in the three subfamilies are striking and clear-cut for the large majority of genera, so that ample justification can be had for division of the Leguminosae into three families, the Mimosaceae, Caesalpiniaceae, and the Papilionaceae or Fabaceae. Many of the world's most important and useful plants hail from the Leguminosae. In the tropics their importance perhaps exceeds that of even the Gramineae (cereal grains, etc.). Aside from supplying timber, food, ornamentals, drugs, poisons, insecticides, resins, shade and ground cover, the Leguminosae are noted for the

peculiar symbiotic relationship of nitrifying bacteria on the roots which makes them very useful for soil improvement.

In many tribes generic differences are exceedingly obscure and undependable, while in others they are sharply marked. Parallel evolution among genera and a multitude of exceptions to the characters on which they are based make it nearly impossible to form simple yet infallible keys. In the keys to the genera of Leguminosae in Panama an effort has been made to avoid obscure characters and those not likely discernible in herbarium material. It is fully realized that some of the distinctions will not always hold when species and genera outside the range of the flora are considered, nor can use of legume characteristics as the sole distinction be avoided in every case.

KEY TO THE SUBFAMILIES

a. Flowers regular, valvate (rarely imbricate) in bud, usually sympetalous; stamens frequently many and long-exserted, giving a delicate "fluffy" appearance to the head or spike; leaves twice-pinnate except in *Inga* and a few species of *Pithecolobium*..... MIMOSOIDEAE

aa. Flowers irregular, imbricate in bud, polypetalous, petals unequal; stamens typically 10 or fewer, mostly briefly exserted or not exserted, rarely in heads or "fluffy" spikes; leaves twice-pinnate only in a few genera.

b. Upper petal within the others in bud; flowers not papilionaceous; stamens usually free; leaves sometimes twice-pinnate (CAESALPINIEAE)..... CAESALPINOIDEAE

bb. Upper petal exterior in bud; flowers typically papilionaceous; stamens except in one tribe united below; leaves never twice-pinnate..... PAPILIONOIDEAE

Subfamily MIMOSOIDEAE (Mimosaceae of many authors)

Trees, shrubs, vines or herbs, variously armed or unarmed. Leaves twice-pinnate (except for *Inga* and a few species of *Pithecolobium* in which the leaves are once-pinnate), usually large, in most genera bearing a gland or glands on the petiole and/or rachis, in some genera sensitive (folding at night or when disturbed), the pinnae normally opposite; leaflets large and few or more frequently small and numerous; petiole usually conspicuously pulvinate. Inflorescence commonly of axillary, pedunculate heads, umbels or spikes, these often borne subterminally from non-foliate nodes and hence constituting a terminal raceme or panicle, usually colorful and ornamental. Flowers usually small, densely clustered, commonly 5-parted, regular, usually complete, rarely imperfect, sessile or less frequently pedicellate, often fragrant; calyx synsepalous, valvate in bud or rarely imbricate, usually small, sometimes minute; corolla sympetalous or polypetalous, usually exceeding the calyx, ordinarily valvate; stamens few or many, free or united, long-exserted, usually the most conspicuous and colorful part of the flower; anthers minute to moderate, gland-tipped or eglandular; ovary 1-carpellate, mostly symmetrical, free, stipitate or sessile, glabrous or pubescent, the style simple and about equalling the stamens. Legume very variable, flat and thin to fleshy and torulose, variously dehiscent or rarely even indehiscent.

A distinctive subfamily well represented in the tropics, especially in the New World. Many genera are nearly pantropical and only a few are confined to either

the Old or New Worlds. A number of species are large trees of ornamental and economic importance. Other species are pestiferous armed weeds. The MIMOSOIDEAE as a whole are usually distinguishable without difficulty by the "fluffy" heads or spikes of clustered, regular flowers with long-exserted stamens.

Most genera of the MIMOSOIDEAE are extremely difficult taxonomically. Parallel evolution, omnipresent variability, and repeated intergradation are the rule rather than the exception. As a result, numerous segregate genera have at various times been proposed, which can scarcely serve any practical purpose. It is difficult enough to recognize the traditional genera of Willdenow and Bentham without including *ad infinitum* the many possible segregable "genera" usually based upon a single difference (this typically in the legume and uncorrelated with distinctive vegetative or floral characters). Such segregates cannot be adequately separated in a key to the genera. It is perhaps significant that the best-versed students of the group, preeminently Bentham, have refrained from inordinate segregation and dependence upon legume characteristics. Willdenow had established legume characters as primarily definitive of most genera, and indubitably such characters are valuable taxonomically. Yet they would seem to have been overstressed. Ample collections of specimens in fruit (seldom sufficient from the tropics, as most specimens of the usually meagre collections consist of flowering material alone) seem to present the intergradation and variability commonly met with in this subfamily.

The outstanding work on the MIMOSOIDEAE is Bentham's classical "Revision of the Suborder Mimoseae" (Trans. Linn. Soc. 30:335–664. 1875), and his treatment of the subfamily for Martius' 'Flora Brasiliensis.' More recent work in the group has been carried on by Ducke, Pittier, Taubert, and others, in a number of publications, while floristically the MIMOSOIDEAE have been treated for North America by Britton and Rose (N. Am. Fl. 23:1–194. 1928), for Colombia by Britton and Killip (Ann. N. Y. Acad. Sci. 35:101–157. 1936), for Peru by Macbride (Field Mus. Publ. Bot. 13:1–113. 1943), and for Guatemala by Standley & Steyermark (Fieldiana: Botany 24:1–88. 1946). In spite of this generous attention a great deal of uncertainty still exists and a need for monographic study of the genera is evident.

a. Stamens united into a short or long tube, usually many, rarely (viz. *Enterolobium*) as few as 10; flowers generally rather large, the sympetalous corolla frequently 4–5 mm. long or longer.
  b. Leaves once-pinnate, 2-ranked; flowers whitish..... 1. INGA
bb. Leaves twice-pinnate (except few species of *Pithecolobium* which then have the leaves few-ranked), mostly few-ranked; flowers sometimes white or cream but often pink.
  c. Either the petiole or rachis or both gland-bearing (the gland sometimes obscure in *Albizzia*); legume various but not elastically dehiscent from above.
    d. Petiolar glands lacking or borne only at the apex of the petiole at or just below insertion of the pinnae; legume relatively slender and thick, often torulose, rarely septate, usually dehiscent and pulpy, the seeds usually longitudinal; corolla usually more or less tubular and greatly exceeding the calyx..... 2. PITHECOLOBIUM
dd. Petiole bearing a gland or glands (except obscure in *Albizzia*

carbonaria), these usually near or below the middle; legume flat and thin but moderately broad, indehiscent or tardily dehiscent, scarcely pulpy, the seeds transverse; corolla (except few species of *Pithecolobium*) funnelform, usually only about twice as long as the calyx.

e. Legume circinate to arcuate, somewhat fleshy, septate or falsely septate; pinnae and leaflets many (leaflets 10–60 pairs per pinna); leaflets shorter than 4 mm. or longer than 8 mm., or if 5–7 mm. long the midvein nearly central.

f. Legume about 1 cm. wide, arcuate or somewhat coiled and twisting in dehiscence, falsely septate; leaflets 5–10 mm. long, the costa nearly central; flowers, where known, essentially glabrous; 2 or 3 species only ..... 2. PITHECOLOBIUM

ff. Legume 2 or more cm. wide, circinate or reniform, coiled into a complete or nearly complete circle, septate; leaflets shorter than 4 or longer than 8 mm., the costa excentric; flowers tomentulose ..... 3. ENTEROLOBIUM

ee. Legume straight or nearly so, thin and dry, not septate; pinnae and leaflets usually fewer (leaflets less than 10 pair per pinna except in 2 species, these with leaflets 5–7 mm. long, their midveins excentric) ..... 4. ALBIZZIA

cc. Petiole and rachis both eglandular; legume elastically dehiscent from above.

d. Inflorescence capitate; stamens many ..... 5. CALLIANDRA

dd. Inflorescence spicate; stamens 5 plus 5 staminodia ..... 16. PENTACLETHRA

aa. Stamens free or united only at the extreme base, except in *Acacia* 10 or fewer; flowers generally rather small, the corolla sympetalous or polypetalous and usually considerably less than 5 mm. long.

b. Herbs, vines, shrubs or trees, seldom aquatic or of swamp habitat; all flowers visibly similar; stems generally lenticellate or armed; legume various.

c. In Panama inflorescence capitate or very short-spicate (except few species of *Acacia* which then have large, hollow, stipular spines); anthers eglandular (rarely glandular in *Acacia*).

d. Petals more or less united (divided almost to base in species of *Acacia* with pedicellate flowers); anthers minute (fraction of a mm. long); flowers usually very small; plants frequently armed.

e. Unarmed or armed, the armament frequently of stipular spines; stamens usually more than 10; petiole and rachis frequently glandular, without nodular apicules; legume unarmed .. 6. ACACIA

ee. In Panama stems armed with scattered, recurved thorns (except sometimes *M. pusilla*); stamens few, usually 10 or fewer, petiole and rachis eglandular but commonly with nodular apicules; legume usually aculeate.

f. Legume flat, oblong or broad, transversely articulate (in Panama); lower flowers of head rarely unisexual; pinnae and leaflets various but often not as below ..... 7. MIMOSA

ff. Legume terete or turgid, usually narrowly linear, continuous; lower flowers of head unisexual; pinnae few to several rather remote pairs, with many leaflets ..... 8. SCHRANKIA

dd. Petals free; anthers comparatively large (usually ½–1 mm. long); flowers small; plants unarmed.

e. In Panama small shrubs or subherbs; stipules setiform, subpersistent; heads with fewer, erect flowers, the peduncular torus little expanded; legume scarcely 5 mm. wide ..... 10. DESMANTHUS

ee. Large shrubs or trees; stipules ovate or caducous; heads orbicular, from an expanded peduncular torus; legume almost 20 mm. wide ..... 11. LEUCAENA

cc. In Panama inflorescence elongate-spicate; anthers gland-bearing, at least in bud.

d. Leaves and inflorescences on condensed short-shoots; petals pilose within; stems with "nodular" spines ..... 12. PROSOPIS

dd. Lacking short-shoots; petals glabrous; armament, if any, of scattered thorns.
e. Trees or shrubs; leaflets less than 15 mm. long, numerous; legume not breaking transversely.
f. Leaflets mostly alternate; legume indehiscent, unarmed..... 13. STRYPHNODENDRON
ff. Leaflets mostly opposite; legume dehiscent; unarmed or aculeate.
g. Usually aculeate; petiole usually glandular; calyx-lobes valvate; flowers with 10 stamens, lacking staminodia; legume smaller, thinner..... 14. PIPTADENIA
gg. Unarmed; petiole eglandular, calyx-lobes imbricate; flowers with elongate staminodia and 5 stamens; legume large, ligneous..... 16. PENTACLETHRA
ee. Large vine-like plants, often tendriled; leaflets longer than 15 mm., few; legume valves eventually breaking into segments..... 15. ENTADA
bb. Herbs or subshrubs, of swampy habitats or even free-floating; lower flowers of head with large, petaloid staminodia, visibly quite different from upper perfect flowers; stems unarmed, not lenticellate; legume short, broad, flat, unarmed, glabrous..... 9. NEPTUNIA

1. INGA Scop.

INGA Scop. Introd. Hist. Nat. 298. 1777.

Amosa Neck. Elem. 2:459. 1790, fide Dalla Torre & Harms.
Torealia Nor. in Verh. Batav. Gen. 5, Art. IV. 4. 1790, fide Dalla Torre & Harms.
Ingaria Raf. Sylva Tellur. 119. 1838.
Feuilléea O. Ktze. Rev. Gen. Pl. 1:182. 1891, in part.

Unarmed trees or shrubs, the branchlets usually pubescent when young and noticeably lenticellate. Leaves of moderate size to very large, 2-ranked, simply compound, the leaflets 2–many pairs; petiole usually short, only rarely alate; rachis short or elongate, unwinged or alate, almost invariably bearing subcupuliform, sessile or less frequently stipitate glands between insertion of the petiolules; leaflets entire, rather small to very large, frequently pubescent, the veins normally prominent below; stipules mostly caducous; petiolules short. Inflorescence of 1 to few pedunculate spikes from the axils, or paniculate by insertion of spikes from terminal or subterminal defoliate nodes; peduncular portion of spikes elongate to almost obsolete, the floriferous portion elongate and lax to condensed and clavate, capitate or umbellate; pedicels prominent in only a few species; bracts usually inconspicuous, caducous or subpersistent. Flowers white or whitish, regular, perfect, typically Mimosaceous; calyx cupular or tubular, very small to quite large, frequently pubescent, 5-toothed; corolla sympetalous, tubular or funnelform, short and small to very elongate, usually pilose without, 5-lobed; stamens many, exceeding the corolla, the filaments united below into a staminal tube; ovary glabrous or pubescent; style elongate, usually equalling or slightly exceeding the stamens, sometimes capitellate. Legume from short and flat to elongate and subterete, glabrous or pubescent, the margins frequently prominent.

Distribution: New World tropics and subtropics; center of distribution apparently northern South America.

Few genera exhibit the variability found in *Inga*, and the difficulty in organizing the species into groups or workable keys. Sections originally proposed by

Bentham and followed by later authors often fail to hold with the accumulation of additional species and especially more material of many problematical or only partially known species. It seems rather futile to try to retain clear-cut sections within the genus at the present time, and a "natural" key must be sacrificed to a large extent so that certain "artificial" distinctions may make it workable. Thus winging of the leaf rachis may not be a fundamental distinction, being possessed by or lacked by closely related species; but yet no character seems as usable for primary breakdown of the genus. Likewise absolute flower size and leaflet size, although undoubtedly somewhat variable with changing environmental conditions, are often more useful characters than are such extremely variable structural features as comparative length of staminal tube, shape and size of rachial glands or (in many species) number of leaflets per leaf. Legume characters are probably useful, but the lack of mature fruiting material of most species makes them impractical as a sole basis of segregation. Doubtless when fruiting material becomes as frequent as is flowering material today, variability in legume will become as noticeable as is variability in flower. Many species grade into others, and there is every reason to suppose that hybridization occurs in a number of species. Several rather well-defined complexes are discernible in the genus; and it is my belief that within these, species should be regarded in as broad a sense as possible and that considerable condensation is in order. Little correlation or condensation outside of Panama is attempted here because of the lack of many types in this hemisphere. Frequently in discussions at the end of the species descriptions, suggestions of similarity or relationship with extra-Panamanian species are given. Future collections may link new species or varieties described to previously known species, but at present it would scarcely seem advisable to lump all such divergent specimens into known categories without intermediate specimens bridging the gap.

Bentham's "Revision of the Suborder Mimoseae" (loc. cit. 1875) is a landmark in the classification of the genus, but at that date, of course, Bentham lacked the quantity of specimens needed to show intergradation of related "species." Pittier has worked with the genus to a considerable extent, introducing a number of new species and discussion of many others. His revision of the genus (Contr. U. S. Nat. Herb. 18:173–224. 1916) seems scarcely conservative enough, and many of his species are probably not valid segregates. This treatment was without keys, and is quite difficult to use for general determinative work. Pittier's "The Middle American Species of the Genus Inga" (Jour. Dept. Agr. Porto Rico 13:117–177. 1929) is a more usable appraisal, correcting many of the deficiencies of the earlier work. Unfortunately, Bentham's sections are more or less rigidly adhered to, and the keys are not easily workable. Pittier can be excused for having difficultly workable keys in a genus such as *Inga*, but it might have been wiser to seek a substitute for the legume characters needed to determine section and series. The treatment accorded *Inga* by Britton and Rose (N. Am. Fl. 23:2–16. 1928) is from the practical standpoint almost useless. Seldom will the key work, and many segregations appear untenable. Britton and Killip follow somewhat the same system in

their "Mimosaceae and Caesalpiniaceae of Colombia" (Ann. N. Y. Acad. Sci. 35:110–124. 1936). Macbride's "Flora of Peru—Leguminosae" (Field Mus. Publ. Bot. Ser. 13:6–47. 1943) and Standley and Steyermark's "Flora of Guatemala" (Fieldiana: Botany 24:34–46. 1946) seem to give a more conservative treatment for their areas. Ducke (Arch. Jard. Bot. Rio de Janeiro 4:19. 1925; 5:119. 1930; 6:13. 1933) has treated the species of *Inga* in the lower Amazon valley.

a. Leaf rachis winged, at least in part.
  b. Wing of rachis nearly obsolete; leaflets mostly less than 6 cm. long, subglabrous, blunt; legume flat, oblong, less than 4 times as long as broad; known only from the type (in fruit) ..... 1. I. DAVIDSONIAE
  bb. Rachis wing usually prominent; leaflets in most species much larger and frequently heavily pubescent; legume except in one or two species several times longer than broad.
    c. Flowers unusually large or gross; calyx funnelform or campanulate, mostly 10–15 mm. broad apically; legume flat.
      d. Calyx and leaflets subglabrous; leaflets 2 pairs ..... 4. I. PORTOBELLENSIS
      dd. Calyx and leaflets usually heavily pubescent; leaflets mostly 4 pairs ..... 6. I. GOLDMANII
    cc. Flowers thinner or more delicate; calyx rarely as much as 6 mm. wide, subtubular or else very small; legume various.
      d. Calyx glabrous or sparingly pubescent.
        e. Leaflets glabrous; inflorescence umbellate or capitate, or very long and laxly spicate.
          f. Inflorescence umbellate or capitate; calyx at least 2 mm. long.
            g. Calyx 2–3 mm. long; flowers long-pedicellate; terminal leaflets usually about 10 cm. long ..... 2. I. MYRIANTHA
            gg. Calyx at least 15 mm. long; flowers short-pedicellate or subsessile; terminal leaflets usually 20–30 cm. long ..... 4. I. PORTOBELLENSIS
          ff. Inflorescence elongate, lax; calyx about 1 mm. long ..... 28. I. MARGINATA
        ee. Leaflets pubescent at least on the veins; inflorescence a dense, short spike.
          f. Floral bracts 10–20 mm. long, persistent; stipules subpersistent; calyx and lower leaf surface with darker "glandular" dots ..... 11. I. PANAMENSIS
          ff. Floral bracts minute or caducous; stipules caducous, at least in age; plant not noticeably "glandular" dotted.
            g. Spikes conspicuously pedunculate; leaflets mostly acuminate; corolla shorter than 8 mm., or longer than 35 mm.
              h. Corolla never longer than 8 mm.; branchlets cinereous-pubescent; leaflets lightly pubescent (except on veins); legume subglabrous, blackish ..... 5. I. DENSIFLORA
              hh. Corolla longer than 35 mm.; branchlets dark-tomentose; leaflets rather heavily pubescent; legume densely ferruginous-strigose ..... 8. I. MUCUNA
            gg. Spikes subsessile, the condensed floriferous portion obscuring the peduncular portion; leaflets acute to rounded, rarely acuminate; corolla 13–16 mm. long ..... 9. I. HAYESII
    dd. Calyx noticeably pubescent, usually tomentose.
      e. Inflorescence umbellate, the flowers slenderly long-pedicellate ..... 2. I. MYRIANTHA
      ee. Inflorescence spicate, the flowers sessile or rarely short-pedicellate.
        f. Leaflets glabrous or very sparingly appressed-hirsute; young branchlets markedly angled, quadrangular; floral bracts ovate, subpersistent, about 1 cm. long; legume flat ..... 10. I. SPECTABILIS
        ff. Leaflets pubescent at least on the veins; young branchlets less markedly angled, subterete; floral bracts either nearly linear, or else small or caducous; legume tetragonal or subterete.

g. Floral bracts 10–20 mm. long, subpersistent; legume broader, tetragonal, glabrous; leaflets minutely "glandular" below.
h. Leaflets mostly 3 (or fewer) pairs; petiole scarcely winged; terminal rachial internode more prominently winged than penultimate.
i. Corolla about 1.5 cm. long; staminal tube barely exserted; leaflet sparingly pubescent or subglabrous, even on the veins..... 11. I. PANAMENSIS
ii. Corolla about 2 cm. long, the constricted tube obscured in bud by the calyx; staminal tube scarcely exserted; leaflet usually lightly hirsute or pilose over entire lower surface..... 11a. I. PANAMENSIS var. PITTIERI
iii. Corolla about 3 cm. long, the bud noticeably clavate; staminal tube well exserted; leaflet usually not prominently pubescent except on the veins..... 11b. I. PANAMENSIS var. CLAVATA
hh. Leaflets 4 pairs; petiole prominently winged; rachis about equally winged on all rachial internodes..... 12. I. ALATOPETIOLA
gg. Floral bracts inconspicuous, small or caducous; legume slender, subterete or angled, tomentose; leaflets eglandular on lower surface.
h. Tomentum of branchlets, petioles and young legume subhirsute, rubiginous or dark-ferruginous; buds and flowers dark, usually ferruginous or ferruginous-golden.
i. Tertiary veins of leaflets conspicuously reticulate; calyx usually 3–6 mm. long; mature stamens 20–25 mm. long; rachis frequently scarcely winged except on terminal rachial internode, or this markedly larger than wing of lower rachial internodes..... 13. I. OERSTEDIANA
ii. Tertiary veins of leaflets inconspicuous; calyx 8–10 mm. long; mature stamens almost 45 mm. long; rachis winged about equally on all or most rachial internodes..... 16. I. PAUCIFLORA
hh. Tomentum of branchlets, petioles, and young legume of shorter hairs, cinereous-ferruginous; buds and flowers light, cinereous or cinereous-golden.
i. Leaflets ovate to elliptic or obovate, 5–8 cm. wide; flowers less robust, the calyx normally less than 8 mm. long.
j. Flowers rather large, the calyx usually 7–8 mm. long and the corolla almost 2 cm. long; branchlets less prominently lenticellate..... 14. I. EDULIS
jj. Flowers small, the calyx about 4 mm. long, the corolla about 8 mm. long; branchlets densely raised-lenticellate..... 14a. I. EDULIS var. MINUTULA
ii. Leaflets narrowly ovate-lanceolate to obovate-lanceolate, 2–5 cm. wide; flower stouter, the calyx 10–20 mm. long, or if only 8 mm. long the branchlets subhirsute.
j. Leaflets mostly more than 4 pairs; calyx 10–20 mm. long; branchlets tomentose..... 15. I. SPURIA
jj. Leaflets 3 or 4 pairs; calyx 8–10 mm. long; branchlets subhirsute..... 16. I. PAUCIFLORA
aa. Leaf rachis unwinged or merely marginate.
b. Leaflets 5 or more pairs.
c. Pubescence setose or villous, of very long hairs; flowers long-pedicellate..... 17. I. SAFFORDIANA
cc. Pubescence, if any, tomentose, of short hairs; flowers sessile.
d. Leaflets moderately appressed-pubescent to tomentose below; leaflets mostly broadest at or below the middle; flowers larger, the calyx 5–12 mm. long.

e. Leaflets moderately pubescent; branchlets ferruginous-tomentose; legume somewhat flattened? ..... 18. I. MULTIJUGA
ee. Leaflets heavily pubescent; branchlets dark-rubiginous-tomentose; legume terete?; known only from the incomplete type.... 19. I. COCLEENSIS
dd. Leaflets subglabrous or scatteringly puberulent; leaflets broadest above or below the middle; flowers small, the calyx 3–4 mm. long.
e. At least the terminal leaflets broadest above the middle; leaflets usually 6 pairs; flower rather large (calyx 3–4 mm., corolla 7–8 mm. long), densely puberulent ..... 20. I. RUIZIANA
ee. Leaflets broadest at or below the middle; leaflets 4–5 pairs; flower smaller (calyx about 2 mm., corolla 4–6 mm. long), lightly puberulent ..... 21. I. MICROSTACHYA
bb. Leaflets 3 (rarely 4) or fewer pairs.
c. Flowers large and stout, the corolla 15–25 mm. long, the calyx either about 9 mm. long or else woolly and nearly 5 mm. wide.
d. Leaflets 4 pairs; calyx cupular, lanose-tomentose; floral bracts small, caducous ..... 7. I. STANDLEYANA
dd. Leaflets 1–3 pairs; calyx somewhat tubular, not woolly; floral bracts 10 mm. long or longer, subpersistent.
e. Leaflets glabrous or very sparingly appressed-hirsute; young branchlets markedly angled; floral bracts ovate; legume flat.... 10. I. SPECTABILIS
ee. Leaflets pubescent at least on the veins; branchlets subterete; floral bracts linear; legume tetragonal ..... 11a. I. PANAMENSIS VAR. CLAVATA
cc. Flowers small, the corolla seldom more than 10 mm. long, the calyx 1–7 mm. long and up to 2 mm. wide.
d. Floriferous portion of spike short, condensed, usually less than 1 cm. long.
e. Inflorescence capitate or umbellate, bearing flowers from the terminal few mm.
f. Flowers pubescent, somewhat pedicellate; leaflets rarely as much as 18 cm. long, the terminal ones usually 12–16 cm. long.
g. Pubescence of twigs and inflorescence setose or villous, of very long hairs; pedicels almost 2 cm. long; legume dark villous ..... 17. I. SAFFORDIANA
gg. Pubescence of young twigs and inflorescence tomentose, of short hairs; pedicels scarcely 0.5 cm. long; legume tomentulose.
h Pedicels as long as the calyx; calyx somewhat expanding basally and subcampanulate ..... 22. I. ROUSSOVIANA
hh. Pedicels conspicuously shorter than the calyx; calyx funnelform, narrow basally ..... 23. I. WILLIAMSII
ff. Flowers glabrous or subglabrous, prominently pedicellate or sessile; leaflets either very large, 13–40 cm. long, or very small, 2–10 cm. long.
g. Flowers prominently pedicellate; leaflets small, 2–10 cm. long, usually 1–2 pairs ..... 3. I. HETEROPHYLLA
gg. Flowers sessile or subsessile; leaflets large, 13–40 cm. long, usually 3 pairs ..... 24. I. GIGANTIFOLIOLA
ee. Inflorescence short-spicate, bearing flowers for about 1 cm. of its length.
f. Leaflets 2–3 pairs; twigs and leaflets strigose-puberulent; calyx 3–5 mm. long ..... 25. I. PUNCTATA
ff. Leaflets 4–5 pairs; twigs and leaflets subglabrous; calyx about 2 mm. long ..... 21. I. MICROSTACHYA
dd. Floriferous portion of spike elongate, lax, usually about 8 cm. long.
e. Rachis unwinged, scarcely marginate; leaflets usually broadly elliptic, bluntly short-acuminate.
f. Leaflets 4–12 cm. long and 1.5–5.5 cm. wide, mostly 2 pairs; stipules and stipule-like bracts not apparent, or at most 6 mm. long ..... 26. I. LAURINA

ff. Leaflets larger, the terminal pair about 15 cm. long and 6–7 cm. wide, mostly 3 pairs; stipules and stipule-like bracts of new growth and buds conspicuous, mostly 8–12 mm. long ..... 27. I. CALDASIANA

ee. Rachis briefly winged or decidedly marginate terminally; leaflets usually narrowly elliptic or elliptic-lanceolate, sharply long-acuminate ..... 28. I. MARGINATA

1. INGA DAVIDSONIAE Standl. in Field Mus. Publ. Bot. 22:79. 1940.

Small tree, the branchlets ferruginous-tomentose becoming glabrate and noticeably lenticellate with age. Leaves comparatively small, about 10-foliolate; petiole 5–15 mm. long, terete, lightly tomentose; rachis 3–7 cm. long, very narrowly alate (wing most conspicuous on uppermost foliolar internode), pubescent although lightly so on the wings, bearing small, sessile, cupuliform glands between insertion of the petiolules; leaflets unusually small, oblong or elliptic to ovate-lanceolate, about 7 cm. long and 3.5 cm. wide in largest (terminal) leaflets, scarcely 2 cm. long and 1 cm. wide in smallest (basal) leaflets, subtruncate to bluntly acute apically, rounded or obtuse and somewhat inequilateral basally, coriaceous, subglabrous except on the midvein and glossy above, noticeably pubescent on the veins and dull below; stipules caducous. Inflorescence an axillary, pedunculate spike nearly 5 cm. long, the floriferous portion little more than 1 cm. long. Flowers not known. Legume oblong, about 12 cm. long and 5 cm. wide, flat, more or less truncate apically and basally, transversely striate, tomentose becoming subglabrate in age, the valvular margins sulcate.

Known only from the type.

CHIRIQUÍ: Volcán de Chiriquí, *Davidson 943*.

The leaflets of this species have a "*Pithecolobium* appearance," but the legume scarcely resembles any species of that genus with once-pinnate leaves. Lack of flowers prevents accurate comparison with other species of *Inga*, but the small, coriaceous, glossy, rather variably shaped leaflets are distinctive. The legume much resembles that of *I. monticola* Pittier.

2. INGA MYRIANTHA Poepp. & Endl. Nov. Gen. & Sp. 3:77, *pl. 289*. 1845.

Inga gracilipes Standl. in Jour. Wash. Acad. 15:101. 1925.
Inga Lawranceana Britt. & Killip, in Phytologia 1:23. 1933.

Small tree, the branchlets subglabrous and very densely white-lenticellate. Leaves of moderate size, 4- (rarely 6- or 2-) foliolate; petiole 1–3 cm. long, terete basally, prominently marginate or alate apically, glabrous or somewhat puberulent above; rachis 2–5 cm. long, essentially glabrous, alate between leaflet pairs (wing broadest at apex of rachial internode, narrowing baseward), bearing prominent patelliform or subcupulate glands above at the rachial nodes; leaflets usually 2 pairs, mostly elliptic, the terminal pair about 10 cm. long and 4 cm. wide, the basal pair half or less this size, obtuse or broadly cuneate basally, short-acuminate apically, completely glabrous, lustrous, the prominent lateral veins about 5 pairs; stipules linear, about 5 mm. long, caducous. Inflorescence of pedunculate umbels, axillary

or subterminal from young defoliate nodes; peduncles 2–5 cm. long, almost glabrous; pedicels slender, almost 1 cm. long, lightly puberulent; floral bracts linear-clavate, 2–3 mm. long, subpersistent. Flowers delicate, greenish-white; calyx cupuliform-tubular, about 3 mm. long, subglabrous or lightly puberulent, the teeth triangular and about 0.5 mm. long; corolla tubular-funnelform, about 8 mm. long, slightly broadened apically, glabrous except puberulent on the lobes, substriate; stamens 2–3 cm. long, the staminal tube exserted. Young legume flat, subglabrous, margined.

Panama.

CANAL ZONE: Barro Colorado Island, *Bangham 488, 522; Salvoza 929; Woodworth & Vestal 587;* France Field, *Standley 30353.*

An interesting species apparently without close affinities in Panama, distinguished by the graceful, prominently pedicellate flowers. The species has not previously been reported from Central America as *I. myriantha.* South American material of the species varies in flower size, and some Peruvian specimens have flowers almost ⅓ again as large as the specimens here cited. Other Amazonian material seems identical with the Panamanian specimens. In deciding that *I. gracilipes* is not distinct from *I. myriantha,* it has been necessary for comparison to rely on the original description and illustration, plus limited herbarium material of *I. myriantha,* the type specimen not being available.

3. INGA HETEROPHYLLA Willd. Sp. Pl. 1020. 1806.

Mimosa Parae Poir. in Lam. Encycl. Meth. Suppl. 1:44. 1810.
Inga umbellata G. Don, Gen. Hist. Dichl. Pl. 2:391. 1832.
Inga protracta Steud. in Flora 26:758. 1843, fide Benth.

Shrub or small tree, the branchlets puberulent when very young, soon becoming glabrous, lenticellate. Leaves moderate, the leaflets 1–2 (sometimes more?) pairs; petiole short, usually less than 1 cm. long, glabrous in age, subsulcate above, eglandular; rachis frequently exceeding the petiole, unwinged, glabrous, bearing cylindric glands at insertion of the pairs of petiolules, at least in the larger leaves; leaflets elliptic, 2–10 cm. long and 1–4 cm. wide, in quadrifoliolate leaves the basal pair of leaflets the smaller, acuminate and markedly attenuate apically, cuneate basally, glabrous, the venation reticulate and prominent below; stipules linear, about 2 mm. long, caducous. Inflorescence of axillary pedunculate umbels, slender and delicate; peduncles up to 2 cm. long; pedicels 4–12 mm. long, glabrous. Flowers moderate; calyx cupulate, scarcely 1 mm. long, glabrous; corolla tubular-funnelform, 5–6 mm. long, glabrous, the tube about twice as long as the lobes; staminal tube exserted. Legume linear, up to 13 or 14 cm. long and about 17 mm. wide, flat, glabrous, nearly straight, short-stipitate.

Panama to middle South America.

COCLÉ: Bismarck, *Williams 600.*

The cited specimen, examined for the North American Flora, was found in-

correctly determined as *I. laurina*, and constitutes a new record for *I. heterophylla* north of South America. The specimen is in fruit, but is apparently referable to this species; certainly it is as much so as is South American material of various herbaria commonly passing as *I. heterophylla*. There is some doubt that *I. mapiriensis* Pittier, *I. Jenmani* Sandw., and perhaps other species, can be maintained distinct from *I. heterophylla*. Other species related to *I. heterophylla* are: *I. cynometrifolia* Harms, *I. sertulifera* DC., *I. tarapotensis* Spruce, *I. myriantha* P. & E., and *I. coriacea* (Pers.) Desv.

4. INGA PORTOBELLENSIS Beurl. in Svensk. Vet. Akad. Handl. 1854:122. 1856.

Inga macrophylla Billb. ex Beurl. loc. cit. 123. 1856, fide Ind. Kew.

Tree more or less glabrous throughout, the young branchlets with elongate lenticels. Leaves large, bijugate; petiole usually 2–3 cm. long, winged (the wing narrowing baseward and the petiole subterete basally); rachis usually 6–8 cm. long, spatulate-winged like the petiole, bearing at insertion of the pairs of leaflets an elevated, cupuliform gland, bearing apically in young leaves a (deciduous) mucronate appendage as much as 15 mm. long; leaflets 2 pairs, obovate-oblong, 20–30 cm. long, 10–13 cm. wide in apical pair (basal pair only half as long), obtuse basally, abruptly acuminate apically, darker above than below, glabrous except occasionally puberulent on the costa; stipules ovate-subfalcate, about 16 mm. long, subpersistent. Inflorescence of solitary, axillary, pedunculate heads (or very condensed spikes); peduncle 3–8? cm. long, glabrous; bracts of head ovate or lanceolate, 7–8 mm. long, late-caducous. Flowers short to moderately pedicellate, large and showy; calyx tubular-funnelform, about 25 mm. long, striate, glabrous except pubescent on tips of the lobes; corolla tubular, almost 4 cm. long, glabrous except canescent-pubescent on the lobes; stamens as much as 7–8 cm. long, the staminal tube well-exserted; ovary glabrous. Legume flat, about 16 cm. long and 2.5 cm. wide, arcuate, ligneous, thickened on the margins.

Panama and Costa Rica.

We have examined no Panamanian material (unless *Allen 17282* be this species: see "Specimens of Uncertain Status"). The (European) type, however, is from Porto Bello, province of Colón, Panama. Costa Rican material does not match the original description in some respects, but we accept Pittier's and Britton and Rose's citations as correct for this name. The species seems to be unusual and striking.

5. INGA DENSIFLORA Benth. in Trans. Linn. Soc. 30:617. 1875.

Inga monticola Pittier, in Contr. U. S. Nat. Herb. 18:190, *pl. 96*. 1916.
Inga java Pittier, in Trab. Mus. Com. Venez. 5:261. 1929.

Large, spreading tree about 16 m. tall, the branchlets lightly or moderately cinereous-tomentose. Leaves moderately large, 8-foliolate; petiole scarcely 1 cm. long, terete, tomentose, swollen basally; rachis up to 10 cm. long, narrowly alate

(sometimes obscurely so on lowermost rachial internode), tomentose along the axis, bearing above at the rachial nodes a sessile, patelliform gland; leaflets normally 4 pairs, elliptic to elliptic-lanceolate, 10–20 cm. long and 5–7 cm. wide in the terminal pair, usually short-acuminate apically, obtuse to blunt and somewhat inequilateral basally, heavily pubescent on costa and chief veins, loosely appressed-strigose or subglabrous and "glandular" elsewhere; stipules linear, about 5 mm. long, caducous. Inflorescence of 1–2 pedunculate spikes borne from subterminal axils; peduncle 3–6 cm. long, pubescent; floriferous portion of spike usually 1–3 cm. long, the flowers very congested; bracts small, caducous. Flowers small, white, sessile; calyx tubular-funnelform, about 4 mm. long, subglabrous or sparsely strigose, striate; corolla tubular, 7–8 mm. long, hirsute-strigose; stamens 15 or more mm. long, the staminal tube scarcely exserted. Legume broad, flat, up to 16 cm. long and 5 cm. wide, slightly margined, transversely striate, subglabrous in age, blackish, several-seeded.

Northern South America and Panama.

COCLÉ: Bismarck, *Williams 316*. SAN BLAS: Permé, *Cooper 651*.

The San Blas specimen differs from the Coclé one (type of *I. monticola*) in degree of pubescence, size of leaflet, and in other minor ways. The latter probably reflects intermixture with other species towards the northern extremity of its range. The San Blas specimen is nearly identical with the type of *I. java* (from tree planted for coffee shade in Venezuela).

6. INGA GOLDMANII Pittier, in Contr. U. S. Nat. Herb. 18:198. 1916.

Moderate-sized tree, the branchlets ferruginous-hirsute. Leaves large, mostly 8-foliolate; petiole usually about 1 cm. long, alate, hirsute except lightly pubescent on the wings; rachis up to 20 cm. long, similar to the petiole, the wing about 5 mm. wide from midrachis to margin, bearing short-stipitate, cupuliform glands between insertion of the petiolules; leaflets mostly 4 pairs, ovate to elliptic, up to 25 cm. long and 15 cm. wide, the terminal pair about twice as long as the basal pair, acute and short-acuminate apically, rounded and inequilateral basally, subglabrous above except on the midvein (midvein heavily pubescent and usually bearing 1–2 small glands basally), laxly pubescent below especially on the veins; stipules broadly ovate, caducous in age. Inflorescence a stout terminal or axillary spike, the peduncular portion about 8 cm. long and hirsute, the floriferous portion up to 6 or 7 cm. long; bracts broadly ovate, scarcely 4 mm. long, hirsute, deciduous in age. Flowers very broad and stout; calyx subcampanulate, about 13 mm. long and almost as wide (apically), densely hirsute-tomentose; corolla tubular-campanulate, 2 cm. long or longer, densely villous without; stamens about 6 cm. long, the staminal tube included. Legume flat, about 18 cm. long and 4 cm. wide?, somewhat arcuate, stipitate, densely ferruginous-hirsute, the margins not unduly thickened.

Panama and Costa Rica.

CANAL ZONE: Frijoles, *Allen 922;* Gatún, *Goldman 1866;* Lion Hill Station, S. *Hayes 598;* Monney? Hill, *Lehmann 1001;* near Salamanca, *Steyermark & Allen 16754.*

This species has been segregated from Bentham's original concept of *I. Lindeniana,* and without reference to the (European) type of *I. Lindeniana* it is impossible here to pass judgment on the validity of the segregation. Perhaps the most definitive difference given by Pittier between *I. Goldmanii* and *I. Lindeniana* is the considerably lesser pubescence of the former. Certain herbarium specimens (in fruit) labeled *I. mucuna* are evidently referable here.

7. INGA STANDLEYANA Pittier, in Contr. U. S. Nat. Herb. 18:204. 1916.

Low tree, the branchlets densely dark ferruginous-tomentose. Leaves large, 8-foliolate; petiole 2–4 cm. long, terete, tomentose like the branchlets, swollen basally; rachis about 11 cm. long, unwinged, similar to the petiole, bearing sessile, urceolate glands above between insertions of the petiolules; leaflets 4 pairs, broadly ovate or obovate, about 12 cm. long and 7–8 cm. wide in terminal pair (lowermost pair about ½ as long), rounded or obtuse or briefly acute, and very briefly mucronate apically, obtuse or rounded and somewhat inequilateral basally, pilose below, subglabrous above except tomentose on the costa and chief veins, reticulate, darker above than below; stipules caducous. Inflorescence of 1–2 pedunculate spikes axillary and subterminal from the upper branchlets; peduncular portion 2–4 cm. long, tomentose like the branchlets; floriferous portion equally long, the flowers somewhat distant; floral bracts ovate, 1 mm. long, caducous. Flowers large, sessile; calyx cupular, about 5 mm. long and equally as wide, lanose-tomentose, the teeth scarcely discernible because of the pubescence; corolla funnelform, 17–20 mm. long, gross, lanose-tomentose; stamens about 5 cm. long, the staminal tube barely exserted; ovary white-pubescent along sutural line; style 5 mm. long; stigma capitate. Legume reported flat and densely rufous-pubescent.

Panama.

DARIÉN: La Palma, *Pittier 5496.*

This species is readily distinguished from others in Panama by the gross, woolly flower. It is said to be quite similar to *I. dysantha* of South America, a species of which no specimens have been available for comparison.

8. INGA MUCUNA Walp. & Duchass. in Walp. Ann. 2:459. 1851–52.

Moderate-sized tree, the branchlets dark hirsute-tomentose. Leaves moderate, the leaflets 6- or 8-foliolate; petiole about 2 cm. long, heavily tomentose, terete and unwinged; rachis up to 15 cm. long, with prominent interfoliolar wings about 5 mm. wide from rib to margin, the rib tomentose, the wings more lightly pubescent, with small, sessile, subcupuliform glands between insertion of the leaflets; leaflets apparently 3 or 4 pairs, mostly ovate, up to 15 cm. long and 7 cm. wide terminally, progressively smaller baseward, apically acute and short-acuminate, basally inequilaterally rounded or obtuse, rather heavily pubescent with curved hairs below and above; stipules triangular-ovate, about 6 mm. long, soon deciduous. In-

florescence of 1 to few? pedunculate spikes axillary from the upper leaves, the peduncular portion hirsute-tomentose, about 4 cm. long, the floriferous portion less heavily pubescent, 3–5 cm. long; bracts ovate-elliptic, about 6 mm. long, caducous. Flowers white, very elongate; calyx tubular, 13–17 mm. long, longitudinally striate or sulcate, subglabrous except at the apex of the teeth, the teeth 1–2 mm. long; corolla 4–5 cm. long, pilose without (sparingly so in age), the hairs 3 mm. long or longer, the lobes somewhat flaring, about 5 mm. long; stamens up to 10 cm. long, the staminal tube exserted about 2 cm. beyond the corolla; ovary tetragonal and indented on opposite faces. Legume up to 30 cm. long and 5 cm. wide, usually spirally twisted, densely ferruginous-strigose, the margins deeply sulcate along the line of dehiscence.

Panama; northern South America?

CANAL ZONE: Barro Colorado Island, *Woodworth & Vestal 665.* DARIÉN: Boca de Cupe, *Allen 882;* Sambú River, *Pittier 5525.* PROVINCE UNKNOWN: "Panama," *Duchassaing 81.*

The cited specimens certainly seem to belong to section PSEUDINGA, series LONGIFLORAE as considered by Pittier in his revision of *Inga.* Of this series only one species, *I. mucuna,* is reported north of South America: thus the species' affinities are chiefly South American (Brazil especially). Without fruit as a criterion, a specimen of this species might key to (Pittier's) *I. oophylla, I. Rodrigueziana, I. Rensoni, I. Preussii* or *I. Holtonii,* but it differs from all of these in having the extremely elongate corolla. Brazilian specimens in the herbarium labeled *I. calantha* Ducke (*Krukoff 6204,* fruit only) appear very similar to the Panamanian specimens, and possibly are identical.

9. INGA HAYESII Benth. in Trans. Linn. Soc. 30:617. 1875.

Feuilléea Hayesii Ktze. Rev. Gen. Pl. 1:188. 1891.

Small tree, the branchlets rather heavily pubescent when young becoming glabrous. Leaves moderate, 4- to 8-foliolate; petiole 1–2 cm. long, pubescent especially medianly, narrowly winged except at the extreme base; rachis 2–10 cm. long, similar to the petiole except the rachial internodes prominently alate (wing up to 5 mm. wide measured from midrachis), bearing sessile, patelliform or cupuliform glands between insertion of the petiolules; leaflets 2–4 pairs, ovate, oblong or elliptic, the larger (terminal) ones as much as 15 cm. long and 7 cm. wide, the smaller (basal) ones about 5 cm. long and 2.5 cm. wide, acute, obtuse or even rounded apically, obtuse or rounded basally and not markedly inequilateral, with scattered curved-appressed hairs above and below, the veins prominent below; stipules broadly ovate, 2–3 mm. broad, soon caducous. Inflorescence very condensed, of 1 to few? axillary spikes from the tips of branches, the peduncular portion usually less than 1 cm. long and obscured by the compact floriferous portion 1–3 cm. long; bracts lanceolate, inconspicuous, at most a few mm. long. Flowers whitish, densely compacted; calyx tubular, 6–9 mm. long, subglabrous except for small tufts of hair at the tip of calyx lobes and sometimes the base of

Fig. 75. *Inga Hayesii*

the calyx, longitudinally striate, rather deeply cleft on one or two sides (the teeth thus unequal); corolla tubular-funnelform, 13–16 mm. long, silvery-pilose without, the lobes about 3 mm. long; stamens up to 4 cm. long, the staminal tube included; ovary subglabrous, 4-angled due to lateral indentations; stigma capitellate. Legume linear-oblong, up to 17 cm. long and 2 cm. wide, flattened, yellow-tomentose.

Panama.

CANAL ZONE: Ancon Hill, *Seibert 115;* Fort Kobe road, *Allen 1890;* Miraflores; *P. White 79.* PANAMÁ: Matías Hernández, *Pittier 6714;* Pacora, *Woodson, Allen & Seibert 759;* Pearl Islands, *Allen 2593.*

The cited specimens comprise an entity in many ways imperfectly matching various descriptions of *I. Hayesii.* Nevertheless, knowing the extreme variation and intergradation common in *Inga,* it would be presumptuous to regard them as a different species. The short-pedunculate spike is perhaps the species' outstanding characteristic, and this, along with the subglabrous, striate calyx and relatively light leaf pubescence, tends to distinguish *I. Hayesii* from most (otherwise) similar species. Some specimens of *I. spuria* much resemble the cited specimens except for larger flower size and generally greater leaflet number.

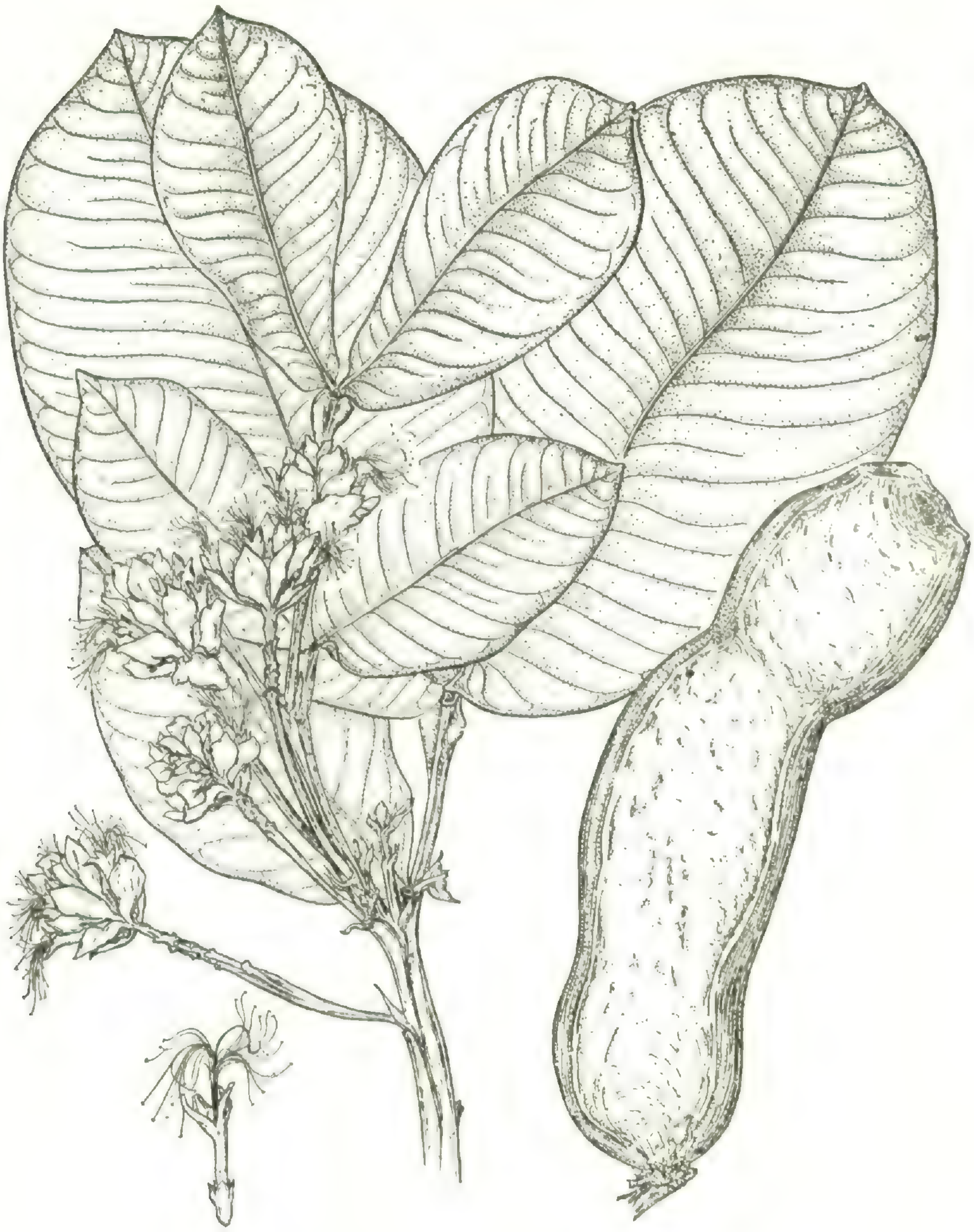

Fig. 76. *Inga spectabilis*

10. INGA SPECTABILIS (Vahl) Willd. Sp. Pl. 4:1017. 1806.

Mimosa spectabilis Vahl, Skr. Natur. Selsk. Kjöb. 2:219, *pl. 10.* 1792.
Inga fulgens Kunth, Mimos. Pl. Legum. 36, *pl. 11.* 1819.
Inga lucida HBK. Nov. Gen. & Sp. 6:287. 1824.
Feuilléea spectabilis Ktze. Rev. Gen. Pl. 1:184. 1891.

Moderate-sized tree, the branchlets lightly pubescent to glabrous and markedly angled, lenticellate. Leaves large, mostly 4-foliolate; petioles scarcely 1 cm. long, angled or short-winged, sometimes puberulent; rachis up to 7 or more cm. long, somewhat puberulent, alate towards the upper part of each rachial internode (the

wing broadest just below insertion of the leaflets), the wing from subobsolete to 7 or 8 mm. wide measured from midrachis, bearing a large, cupuliform or patelliform gland between insertion of the petiolules, usually puberulent at least medianly above; leaflets 1–3 (usually 2) pairs, elliptic or nearly so, up to 25 cm. long and 15 cm. wide in terminal pair, the basal pair smaller (often lacking in herbarium material), rounded to acute apically, more or less obtuse and inequilateral basally, coriaceous, glabrous above in maturity, subglabrous below, the veins impressed above and prominently elevated below, the alternate lateral veins much shorter than the others; stipules linear to linear-lanceolate or linear-oblanceolate, about 1 cm. long, subpersistent. Inflorescence mostly a terminal panicle of pedunculate spikes (the spikes sometimes solitary from an axil), the peduncular portion generally 4–5 cm. long and lightly puberulent, the floriferous portion about 5 cm. long and tomentulose, the flowers more or less congested; bracts nearly elliptic, up to 2 cm. long and almost 1 cm. wide, more or less persistent, tomentulose. Flowers white; calyx tubular-campanulate, about 9 mm. long, pubescent, somewhat cleft to one side, the teeth about 3 mm. long; corolla tubular, about 2 cm. long, tomentose, the lobes somewhat flaring; stamens about 4 cm. long, the staminal tube about equalling the corolla. Legume flat, reported up to 60 cm. long and 7 cm. wide, the margins thick but not elevated, glabrous.

Costa Rica, Panama, northern South America.

BOCAS DEL TORO: Chiriquí Lagoon, *H. von Wedel 2392.* CANAL ZONE: Culebra, *Pittier 2423;* Las Cascadas, *Pittier 3746.* CHIRIQUÍ: trail from San Felix, *Allen 1944.* COCLÉ: Bismarck, *Williams 383, 584.* PANAMÁ: Taboga Island, *Maxon 6922.* WITHOUT LOCALITY: *Cooper & Slater 203.*

11. INGA PANAMENSIS Seem. Bot. Voy. Herald, 117. 1853.

Small tree, the branchlets slender, essentially terete, pubescent when young becoming glabrous in age, conspicuously lenticellate. Leaves large, 2- to 6-foliolate; petiole 4–5 cm. long, terete or somewhat angled above apically, lightly pubescent or nearly glabrous, swollen basally; rachis as long as (or longer than?) the petiole, similar to the petiole except narrowly winged, bearing at insertion of the petiolules small, concave, sessile glands; leaflets mostly 2 pairs in isotype examined, broadly oblong to elliptic-obovate, terminal ones up to 15 or more cm. long and almost 10 cm. wide (basal leaflets ⅔ or less this size), obtuse or rounded and somewhat inequilateral basally, rounded and briefly mucronate apically, glabrous above, scantily pubescent (especially on veins) and "glandular" below, the veins prominently elevated below, the lateral ones about 12 pairs; stipules ovate, about 6 or 7 mm. long, persistent. Inflorescence of axillary, pedunculate spikes 3–7 cm. long; peduncular portion 2–4.5 cm. long, lightly pubescent, striate; floral bracts linear, about 1 cm. long, persistent, lightly pubescent. Flowers moderate, whitish?; calyx cupular-tubular, 5–8 mm. long, lightly pubescent, striate, the teeth prominent and irregular or unequal; corolla tubular-funnelform, about 14 mm. long, golden appressed-pilose; stamens about 4 cm. long, the staminal tube some-

what exserted; ovary nearly glabrous; style exceeding the stamens; stigma capitellate. Legume (reported) up to 15 or more cm. long and about 4 cm. broad, thick, glabrous, the margins very prominent.

Panama.

CANAL ZONE?: Cruces, *Seemann 407*.

Apparently this species has been collected but once. We have examined the Gray Herbarium isotype of the original collection which appears to be an aberrant form of a large Central American complex. The fact that no undoubted second collection has been made, although the type is from a comparatively well-known area, would support the belief in its aberrancy. Yet the name must take precedence over its more common varieties as here interpreted, in spite of being less "typical" of the complex as known in lower Central America than are its varieties. Two pairs of leaflets to the leaf is unusual for the group in Panama, although Mexican material frequently shows this characteristic. A number of specimens have leaves with both 2 and 3 or 3 and 4 pairs of leaflets.

Many taxonomists will doubtless take exception to my condensation and reduction to varietal status (under *I. panamensis*) of numerous "species" of this complex. It is conceded that the types of such varieties scarcely resemble the species, and that certain extremes among them more resemble other accepted species than *I. panamensis*. Yet when all available material is examined, no clear-cut specific demarcation can be found within the complex. After days of fruitless effort attempting such, it was deemed wiser to regard as of varietal status some fairly constant but difficultly distinguishable entities. These embraced most of the species of Pittier's series TETRAGONAE.

One of the entities *(I. panamensis* var. *clavata)* appears fairly clear-cut. It is found throughout Panama (especially in Bocas del Toro) and in Costa Rica. It differs from the species in having a much longer flower, but vegetative differences (except leaflet number) are scarcely apparent. Another less clear entity *(I. panamensis* var. *Pittieri)* is found in central and western (Chiriquí) Panama and adjacent Costa Rica. It has a flower only a little longer than in the species but the leaflet shape is different and its lower surface more heavily pubescent. Like *I. panamensis* var. *clavata*, it normally has 3 pairs of leaflets per leaf.

A third variety *(I. panamensis* var. *Rodrigueziana)*, including a very variable group of "species" and specimens from Costa Rica and Nicaragua to Mexico all grading into one another, is proposed as a convenient catch-all within the complex for northern Central America. The type specimen (for the species from which the varietal name is taken) is quite unlike *I. panamensis*—4 pairs of leaflets, moderately long flowers, heavy pubescence—yet it seems to grade quite imperceptibly into forms scarcely distinguishable from *I. panamensis* var. *Pittieri*. In flower size var. *Rodrigueziana* is intermediate between var. *clavata* and var. *Pittieri*. Some of the synonyms listed for it (viz. *I. Purpusii*) may with further collections merit varietal standing of their own.

All in all, the species and its varieties comprise a difficult complex, on which it is perhaps profitless to devote inordinate time in the attempt to make detailed taxonomic distinctions.

11a. INGA PANAMENSIS Seem. var. **Pittieri** (Micheli) Schery, comb. nov.

Inga Pittieri Micheli, in Bull. Herb. Boiss. 2:446, *pl. 13*. 1894.
Inga Jimeneziana Pittier, in Contr. U. S. Nat. Herb. 18:208. 1916.

This variety differs from the species in having a slightly longer flower (corolla 20 mm. long vs. 14 mm. in species) and in having normally 6 large, tapered, more pubescent leaflets. The legume is linear-oblong, up to 25 cm. long and 2.0–2.5 cm. wide and thick, tetragonal, the valves deeply sulcate medianly (dry material), the juncture of valves slightly protruding from the otherwise flat face presented by the valve margins, essentially glabrous, scarcely stipitate basally.

Fig. 77. *Inga panamensis* var. *Pittieri*

Panama and Costa Rica.

CANAL ZONE: Gatún, *Wetmore & Abbe 34;* Quebrada La Palma, *Dodge & Allen 7340.* CHIRIQUÍ: San Felix, *Pittier 5452.* COCLÉ: *Bismarck 489.*

Fig. 78. *Inga panamensis* var. *clavata*

11b. INGA PANAMENSIS Seem. var. **clavata**, Schery, var. nov.

Arbor ab specie differt foliolis subtus frequenter minus pubescentibus, floribus longioribus, ca. 3 cm. longis, staminibus 7–8 cm. longis, tubo plerumque exsertissimo.

On vegetative characters this variety is scarcely distinguishable from the species and the preceding variety. The flowers, however, are considerably longer than in the species, the corolla-tube extending well beyond the calyx and making the corolla in bud appear clavate. This same difference in degree is seen in the stamens and staminal tube, which are almost twice as long as in the species.

Costa Rica and Panama.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 523; Cooper & Slater 108;* Water Valley, *H. von Wedel 672* (Herb. Missouri Bot. Gard., TYPE), *849, 2749* (Herb. Missouri Bot. Gard., COTYPE). CANAL ZONE: Barro Colorado Island, *Kenoyer 368;* Darién Station, *Standley 31610* (sterile); Empire, *Piper 5112.* COCLÉ: Bismarck, *Williams 589* (sterile)?. DARIÉN: Cituro, *Williams 673.*

Fig. 79. *Inga panamensis* var. *Rodrigueziana*

11c. INGA PANAMENSIS Seem. var. **Rodrigueziana** (Pittier) Schery, comb. nov.

Inga Preussii Harms, in Fedde Rep. Sp. Nov. 13:420. 1914, ex char.
Inga Rodrigueziana Pittier, in Contr. U. S. Nat. Herb. 18:209. 1916.
Inga biolleyana Pittier, loc. cit. 207. 1916.
Inga Purpusii Pittier, loc. cit. 199. 1916.

This variety is distinguished from the species in having a more robust flower approximately 2.5 cm. long, and a more heavily pubescent leaflet (frequently subtomentose below).

In keeping with a very broad interpretation of *I. panamensis,* the synonyms listed above should constitute a variety of that species. This variety is not known to occur in Panama, but is found in southern Mexico, northern Central America, and perhaps aberrantly in Costa Rica (the type of *I. biolleyana* of Costa Rica appears to be but an extreme of this variety). Besides the type specimens of *I. Rodrigueziana* and *I. biolleyana,* specimens examined include:

NICARAGUA: *Baker 35.*
SALVADOR: *Calderón 171; Pittier 1974; Standley 19109.*
GUATEMALA: *Record 47; Tuerckheim (J. D. Smith) 7855.*
MEXICO: *Purpus 6811.*

Inga Preussii, in spite of priority, is not chosen as the name-bringing synonym for the variety for the reason that the type has not been available for examination.

12. INGA **alatopetiola** Schery, sp. nov.

Arbor?, ramulis juvenalibus ferrugineo-pubescentibus; foliis magnis, petiolis ca. 2 cm. longis, prominenter alatis, costa pubescente, rhachibus ca. 15 cm. longis, glandulam substipitatam concavam ad insertionem parium foliolorum ornatis, foliolis 4-jugatis, ovato-ellipticis, ad 20 cm. longis, 8 cm. latis, basalibus parvioribus, breve-acuminatis, basi inaequalitaliter obtusis vel rotundatis, subglabris costa supra excepta, subtus leviter pilosis, nervis subtus prominenter elevatis supra indentatis; inflorescentia axillari, ca. 7 cm. longa, pedunculo ca. 3 cm. longo, ferrugineo-tomentoso; bracteis linearibus, ca. 1 cm. longis persistentibus tomentosis; calyce tubulato, ca. 15 mm. longo, striato, adpresso-piloso, dentibus brevibus; corolla tubulata, ca. 30 mm. longa, dense pilosa; staminibus ca. 5 cm. longis, tubo vix exserto; legumine ignoto.

Tree?, the young branchlets ferruginous-pubescent. Leaves large, once-pinnate, with 4 pairs of leaflets; petiole about 2 cm. long, alate, the wings subglabrous, the axis pubescent; rachis about 15 cm. long, similar to the petiole, prominently winged between all pairs of leaflets, bearing short-stipitate, concave glands at insertion of each pair of leaflets; leaflets ovate-elliptic, terminal pair up to 20 cm. long and 8 cm. wide, basal pair scarcely half this size, short-acuminate apically, inequilaterally obtuse or rounded basally, subglabrous above except on the costa, sparingly pilose below, the veins indented above, elevated below, coarsely reticulate. Inflorescence an axillary pedunculate spike, peduncular portion 3–4 cm. long, ferruginous-tomentose, floriferous portion similar, comparatively few-flowered, bracts essentially linear, densely pubescent, persistent. Flowers large, sessile; calyx tubular, about 15 mm. long, striate, appressed-pilose, the teeth short and somewhat unequal; corolla nearly tubular, about 30 mm. long, densely villous or pilose without, the lobes relatively short and slender; stamens approximately 5 cm. long, the staminal tube barely exserted; style elongate, exceeding the stamens, the stigma capitate. Legume not known.

Panama.

BOCAS DEL TORO: Almirante region, *Cooper & Slater 65* (U. S. Nat. Herb., TYPE).

The type specimen is somewhat fragmentary, but is sufficient to indicate distinctiveness from known Panamanian species. Floral characters indicate affinities with *I. panamensis* (and Pittier's series TETRAGONAE), and future collections may link it to *I. panamensis* var. *Rodrigueziana*. The winged petiole is unusual in *Inga*, and serves, along with the persistent, linear bracts, the large "panamensis-type" flowers, and various leaf characters, to distinguish the species rather easily.

Fig. 80. *Inga Oerstediana*

13. INGA OERSTEDIANA Benth. in Seem. Bot. Voy. Herald, 117. 1852–57.

Feuilléea Oerstediana Ktze. Rev. Gen. Pl. 1:188. 1891.
Inga eriorhachis Harms, in Fedde Rep. Sp. Nov. 13:525. 1915.
Inga cobanensis Pittier, in Contr. U. S. Nat. Herb. 18:188. 1916.
Inga Tuerckheimii Pittier, loc. cit. 192. 1916, based on same type as *I. cobanensis*.
Inga chiriquensis Standl. in Field Mus. Publ. Bot. 22:78. 1940.

Small or moderate tree, the branchlets dark ferruginous-tomentose, becoming less densely so in age. Leaves large, normally 8-foliolate; petioles up to 5 cm. long, terete, densely dark ferruginous-tomentose; rachis up to 15 cm. long, tomentose like the petiole except very lightly so on the wings, conspicuously alate for the uppermost rachial internode, progressively less alate in penultimate and succeeding (lower) rachial internode (s), bearing between insertion of the petiolules large or small sessile glands (or these sometimes lacking), the glands laterally extended and markedly concave; leaflets 4 (sometimes 3 or 5) pairs, asymmetrically elliptic, oblong or ovate, 7–16 cm. long and 3–8 cm. wide, rounded or subtruncate basally, inequilaterally acute apically, lightly pubescent above except on the veins where

heavily so, moderately pubescent below except densely tomentose on the elevated veins, reticulate; stipules caducous. Inflorescence of 1 to few pedunculate spikes from foliate or young defoliate nodes, the spikes 3–7 cm. long, floriferous for the upper 1–3 cm., densely tomentose like the petiole; bracts ovate, small, promptly caducous. Flowers quite congested, white; calyx campanulate-cupuliform, 3–6 mm. long, ferruginous-hirsute or pilose, the teeth somewhat unequal; corolla subtubular, about 1 cm. long, somewhat flaring apically although constricted for the lower half its length; densely ferruginous-hirsute or pilose, the lobes about 2 mm. long; stamens 2.0–2.5 cm. long, the staminal tube included within the corolla; ovary linear, the style exceeding the stamens. Legume apparently linear, 12 or more cm. long and less than 1 cm. wide, subterete and longitudinally sulcate, sessile, ferruginous-tomentose.

Northern Central America, Costa Rica and Panama; northern South America.

CHIRIQUÍ: Bajo Mona, *Davidson 536;* Boquete, *Pittier 3130;* Cerro Punta, *Allen 1573;* Volcán de Chiriquí, *Davidson 928.*

Again it is impossible without reference to the type to establish with certainty the correct name to the specimens cited. If *I. Oerstediana* should prove not to apply, *I. eriorhachis* could be used. Standley and Steyermark (Fieldiana, Bot. 24:40. 1946) consider *I. cobanensis* and *I. Tuerckheimii* as synonyms of *I. Micheliana;* yet it seems hardly possible to regard *I. Micheliana* a synonym of our *I. Oerstediana,* although *I. cobanensis* and *I. Tuerckheimii* likely are this *(I. Oerstediana).* Pittier, among others, separated some of the possible synonyms given above into separate sections of the genus on the basis of fruit characters. Only one of the cited specimens is with fruit, and on vegetative appearance the others seem to be the same species. It would seem that fruit characters have been overstressed in separating the genus into often unworkable sections, especially in that fruiting specimens are so rarely available. Almost certainly when extensive fruiting specimens are gathered, variation and degrees of intermediacy will be found, perhaps indicating fruit characters to be little more reliable and certainly less practical taxonomically than floral and vegetative characters.

14. INGA EDULIS Mart. in Flora 20:Beibl. 113. 1837.

Mimosa Ynga Vell. Fl. Flum. Ic. 11:*t. 3.* 1827, fide Benth.
Inga vera HBK. Nov. Gen. & Sp. 6:289. 1824, non Willd., fide Benth.
Feuilléea edulis (Mart.) Ktze. Rev. Gen. Pl. 1:187. 1891.

Small or medium tree, the branchlets ferruginous-tomentulose, lenticellate and angled or ridged. Leaves large, usually 10- or 12-foliolate; petioles mostly 2–4 cm. long, terete, rufous-tomentose; rachis almost 20 cm. long, tomentose like the petiole, conspicuously alate, the wing usually 5 or more mm. wide on each side of the rachis, bearing prominent, oval, cupuliform or patelliform glands between insertion of the petiolules, the glands broader than long; leaflets 3–6 pairs, apparently most commonly 5 or 6 pairs in Panama, ovate to elliptic, up to 15 cm. long and 5–7 cm. wide in terminal leaflets, usually about ½ as large in basal leaflets,

acute and somewhat acuminate apically, mostly rounded basally, lightly tomentose below especially on the veins, sparsely appressed-pubescent above, the veins elevated and conspicuously reticulate below, conspicuous but not elevated above; stipules caducous, reported about 5 mm. long. Inflorescence generally of a few pedunculate spikes from the leaf axils, or often paniculate by insertion of such spikes at subterminal defoliate nodes; spikes mostly 6–8 cm. long, floriferous for the upper 2–3 cm., the flowers moderately congested; bracts ovate, about 5 mm. long, caducous in age. Flowers white, moderate; calyx turbinate, apparently 7–8 mm long in Panama, appressed short-pilose, the teeth regular and 1–2 mm. long; corolla tubular, almost 2 cm. long, relatively slender and little expanded apically, densely ascending-pilose, the lobes subequal and 2–4 mm. long; stamens mostly 4 cm. (or up to 5 cm.) long, the staminal tube slightly exserted; ovary glabrous, the style slightly exceeding the stamens. Legume as much as 1 m. long and up to 2 cm. wide or wider, ferrugineous-tomentose, somewhat tetragonous or subterete, the margins almost entirely covering the faces.

Mexico to Panama; South America to middle Brazil.

BOCAS DEL TORO: Almirante, *Cooper & Slater 38;* Changuinola Valley, *Dunlap 220;* Chiriquí Lagoon, *H. von Wedel 1000;* Water Valley, *H. von Wedel 1096.*

This species is very variable, and the description given here is mostly drawn from the Panamanian material. Probably synonymous with *I. edulis* are *I. Endlichii* Harms and *I. latibracteata* Harms (ex char.), and possibly a number of other "species" which intergrade with this. The Panamanian specimens cited resemble more closely collections from South America (Amazon Valley) than most collections labeled *I. edulis* from northern Central America and Mexico. Evidently no well-established distinction between *I. edulis* and *I. spuria* has been apparent to most authors. Examination of all available specimens from Mexico to Brazil shows specimens, practically indistinguishable from each other, determined rather indiscriminately as either *I. edulis, I. spuria,* or even other species. *I. edulis* is here interpreted as having a more slender, less stocky corolla and a generally smaller calyx than *I. spuria.* The leaflets likewise appear significantly larger (especially wider) in *I. edulis* than in *I. spuria* (in Panama). The H. von Wedel specimens cited appear somewhat atypical (more leaflets; corolla more elongate).

14a. INGA EDULIS Mart. var. **minutula** Schery, var. nov.

Arbor foliis speciei similibus; inflorescentiis prominentibus, floribus specie multo brevioribus, bracteis obovato-oblanceolatis, 3–4 mm. longis.

Ferruginous-tomentulose tree with large 6- to 10-foliolate leaves. Inflorescence of 1 to few pedunculate spikes 3–8 cm. long (floriferous portion 1–5 cm.) from either foliate or defoliate axils; bracts 3–4 mm. long; flowers small; calyx cinereous, appressed-pubescent, 4 mm. long; corolla cinereous, short-pilose, about 8 mm. long; stamens about 3 cm. long. Legume tetragonal-subterete, 15–20 cm. long, 10–15 mm. wide, brownish-tomentose, somewhat constricted between the seeds, the valves sulcate.

Panama; Honduras?

Fig. 81. *Inga edulis* var. *minutula*

BOCAS DEL TORO: Changuinola Valley, *Dunlap 582.* CANAL ZONE: Barro Colorado Island, *Zetek 3578; Kenoyer 371;* Gamboa, *Allen 1972;* Gorgona, *Pittier 2696.* DARIÉN: El Real, *Allen 968* (Herb. Missouri Bot. Gard., TYPE).

This variety is well marked from the species by the considerably smaller flowers, and is perhaps worthy of specific rank except that it grades somewhat into both *I. edulis* and *I. Oerstediana.* It resembles *I. edulis* var. *grenadensis* Urb., but differs from that variety in the longer inflorescence and the obovate or oblanceolate bracts. The cinereous flower ordinarily serves to distinguish *I. edulis minutula* from *I. Oerstediana.*

15. INGA SPURIA H. & B. ex Willd. Sp. Pl. 4:1011. 1806.

Mimosa spuria Poir. in Lam. Encycl. Meth. Suppl. 1:40. 1810.
Feuilléea spuria Ktze. Rev. Gen. Pl. 1:189. 1891.
Inga fissicalyx Pittier, in Contr. U. S. Nat. Herb. 18:213. 1916.

Small- to moderate-sized tree, the branchlets ferruginous-tomentose, becoming glabrous in age. Leaves moderate to large, with few to several pairs of leaflets;

petiole short, scarcely exceeding 1 cm., tomentose like the young branchlets, terete; rachis up to 15 cm. long, tomentose, conspicuously alate, bearing a small sessile, cupuliform or patelliform gland between insertion of the petiolules; leaflets 4–9 pairs (usually 6 or 7 pairs), ovate-lanceolate to narrowly obovate, the terminal ones 7–15 cm. long and 2–5 cm. wide, becoming progressively smaller downward, the basal pair usually only ¼ the size of the terminal pair, usually acute or slightly acuminate apically, commonly obtuse or narrowly rounded basally, slightly pubescent above, somewhat more heavily so below, the veins prominent below but not above; stipules broadly linear, a few mm. long. Inflorescence of 1–3 pedunculate spikes from each of several leaf axils, the spikes 4–12 cm. long, floriferous in the upper few cm., tomentose, the flowers subsessile to somewhat pedicellate, more or less congested, white; calyx tubular, 10–20 mm. long, 3–6 mm. broad, cinereous- or golden-tomentose, the lobes 3–5 mm. long; corolla usually close to 2 cm. long, pilose without, the lobes 4–5 mm. long and slightly flaring; stamens many, frequently 5–6 cm. long, the staminal tube invested by the corolla. Legume linear, reported up to 30 cm. long and 1.5 cm. wide, subterete or angled, fulvous-tomentose, the margins thickened and expanded over the faces.

Mexico to northern and eastern South America.

CANAL ZONE: Miraflores, *P. White 79;* Sabana of Panama, *Pittier 2538;* Trinidad River, *Pittier 3973;* Victoria Fill, *Allen 1704.* CHIRIQUÍ: Boquete, *Davidson 823.* COCLÉ: La Pintada, *Hunter & Allen 518;* Penonomé, *Williams 137, 334.* HERRERA: Ocu, *Allen 4069.* PANAMÁ: Chepo, *Hunter & Allen 89;* Juan Díaz, *Allen 939;* R. Las Lajas, *Allen 1608;* Las Sabanas, *Standley 31825.* VERAGUAS: Cañazas, *Allen 160.*

A very variable species, forming a vast complex from Mexico through northern South America. It intergrades with other (both doubtful or recognized) species and is difficult to delimit precisely. Single specimens of two extremes of this species may appear quite distinct; yet examination of many specimens will show all degrees of intermediacy and no clear-cut differences. Characters such as absolute calyx size, number and width of leaflets, presence or absence of pedicellar portion of calyx, etc., normally somewhat constant in most species, show little constancy or correlation in *I. spuria.* Three Mexican "species," *I. eriocarpa* Benth., *I. oophylla* Riley, and *I. sciadodendron* Harms, should probably be reduced to synonymy with *I. spuria* and likely combined to form a variety of the species. *I. xalapensis* Benth., of Mexico and Central America as far south as Costa Rica (fide Pittier), is also in all probability *I. spuria* or a variety of it, but it is not listed among the synonyms because the type has not been examined.

Two centers of divergence in this complex seem discernible. One apparently occurs in south-central Mexico, and may be typified as the "*I. eriocarpa* influence." Here the flowers are generally stockier, the leaflets broader, the corolla pubescence less rigid, the legume stout. This would constitute the "variety" above suggested, to which *I. eriocarpa* would bring the oldest name. All degrees of gradation occur to the "typical" *I. spuria.* The "*I. eriocarpa* influence" is particularly noticeable in Mexico and transitionally in Guatemala, but is little apparent in Panama. A

second less clear center of divergence seems to occur near Honduras or British Honduras. Here slender flowers, narrow and peculiarly veined leaflets, and slender legumes are the rule. This influence is probably felt in Panama as well as northern Central America and Mexico. In addition, throughout its range, other species, *I. edulis* particularly, tend to intergrade with *I. spuria*. As with a number of species of *Inga, I. spuria* is sometimes planted for coffee shade.

16. Inga pauciflora Walp. & Duchass. in Linnaea 23:746. 1850.

Small tree, the branchlets ferruginous-tomentose-hirsute. Leaves moderate, mostly 6- or 8-foliolate; petiole short, up to 1.5 cm. long, heavily pubescent like the branchlets, unwinged; rachis up to 8 cm. long, ferruginous-pubescent, alate (the wings, margin to margin, 4–10 mm. broad), bearing a small, sessile, cupuliform gland between insertion of the petiolules; leaflets mostly 3 or 4 pairs, elliptic or nearly so, the terminal pair up to 13 cm. long and 5 cm. wide, the basal pair up to 5 cm. long and 2 cm. wide, acute and often somewhat acuminate apically, subcuneate to rounded basally, appressed-pubescent above, villous-tomentose below especially on the prominent veins; stipules ovate, about 4 mm. long, pubescent, early caducous. Inflorescence 1–2 axillary or terminal pedunculate spikes, the peduncular portion up to 3 cm. long and ferruginous-pubescent, the floriferous portion about as long or slightly longer; bracts very small, short and broad, caducous. Flowers several, white; calyx broadly tubular, 8–10 mm. long, tomentulose, striate; corolla tubular, about 15 mm. long, pilose; stamens almost 4.5 cm. long, the staminal tube included; stigma capitellate. Legume (young) densely ferruginous hirsute-tomentose, terete, becoming sulcate? or possibly flattened? in age.

Panama.

CANAL ZONE: Ancon Hill, *Williams 32;* Barro Colorado Island, *Woodson & Schery 969;* Chiva-Chiva trail, *Piper 5725.* VERAGUAS: Santa Fé, *Allen 4417.*

The *Woodson & Schery 969* specimen is in very young fruit. Judging from this immature fruit the specimen is likely not *I. eriocarpa, I. spuria* or similar species, although certainly the species grades into the *I. spuria* complex. The fruit of *I. pauciflora* has not been known. Bentham regarded *I. pauciflora* as a synonym of *I. vera*, and indeed a number of difficultly separable species might profitably be combined under that older name.

17. Inga Saffordiana Pittier, in Contr. U. S. Nat. Herb. 18:176. 1916.

Small, slender tree, the branchlets dark setose-villous. Leaves large, 8- or 10-foliolate; petiole about 2.5 cm. long, terete, setose or sparsely villous; rachis up to 20 cm. long, unwinged, pubescent like the petiole, bearing long-stipitate glands above at the rachial nodes; leaflets 4 or 5 pairs, oblong to obovate-lanceolate, about 14 cm. long and 4 cm. wide in terminal pair (lowermost pair only ¼–⅕ this size), tapered but blunt basally and inequilateral, acuminate apically, glabrous above, sparsely setose on the margins and veins below, the veins moderately prominent below, the lateral ones arcuate and subconfluent; stipules subulate, up to 12 mm.

long, setose-villous. Inflorescence axillary or borne on older defoliate wood, umbellate, pedunculate; peduncles up to 13 cm. long, villous-setose; pedicels similarly pubescent, almost 2 cm. long; floral bracts similar to the stipules, subpersistent. Flowers incompletely known; calyx apparently 7–8 mm. long, setose-villous, the teeth elongate and narrow; corolla tubular, about 15 mm. long, setose-villous, especially apically. Legume broadly linear, about 30 cm. long and almost 3 cm. wide, cuneate basally, flat and thin, lightly margined, densely dark villous, about 18-seeded.

Panama.

DARIÉN: Sambú basin, *Pittier 5676.*

A distinctive species with unusual pubescence, long-stipitate rachial glands, and long-pedicellate, umbellate flowers.

18. INGA MULTIJUGA Benth. in Trans. Linn. Soc. 30:615. 1875.

Feuilléea multijuga Ktze. Rev. Gen. Pl. 1:188. 1891.

Tree to several m., the branchlets densely ferruginous-tomentulose. Leaves large, with a variable number of leaflets (5–10 pairs, fide N. Am. Fl.), 6–9 pairs in Panamanian specimens seen; petiole less than 2 cm. long, essentially terete, tomentulose like the branchlets; rachis up to 2 dm. long, similar to the petiole, not winged, bearing a sessile, cupuliform gland 1–2 mm. in diameter between insertion of the petiolules; leaflets few to several pairs, oblong or elliptic to occasionally ovate-lanceolate, mostly about 10 cm. long and 3–4 cm. broad in the terminal leaflets, ½ or less this size in the lowermost leaflets, acute or short-acuminate apically, rounded or obtuse and somewhat inequilateral basally, lightly strigose-puberulent or subglabrate above, rather densely pubescent and paler below; stipules apparently ovate, about 2 mm. long, caducous. Inflorescence of pedunculate spikes up to 6 cm. long, solitary, geminate or fasciculate from the axils of the leaves, the floriferous portion scarcely 2 cm. long; bracts ovate, very small, ferruginous-tomentose like the axis. Flowers congested, spicate on the axis, whitish; calyx tubular, up to 12 mm. long (reported as short as 5 mm. in Guatemalan and Costa Rican specimens), usually cleft on one side for as much as ⅓ its length, puberulent or tomentulose without, the teeth minute; corolla elongate, tubular, 20–25 mm. long, appressed-villous without, the lobes about 2 mm. long; stamens many, almost 4 cm. long, united below into a tube about equalling the corolla; style somewhat exceeding the stamens, the stigma expanded. Legume variously reported glabrous or tomentulose?, flat or subterete?, up to 25 cm. long and 1 cm. wide?, the valves expanded and costate at the edges.

Honduras to Panama.

CANAL ZONE: Barro Colorado Island, *Bangham 528;* "Chagres," *Fendler 51;* Margarita Swamp, *Maxon & Valentine 7058.* VERAGUAS: Cañazas, *Allen 154.*

The usual concept of this species seems to include a remarkably variable group of specimens. Certainly various authors have been at great divergence in writing

descriptions of it, and specimens seen show great differences in leaflet number, calyx size, etc. Dimensions given by Pittier (Contr. U. S. Nat. Herb. 18:187) for the *Fendler 51* specimen at the Gray Herbarium in no way approximate those for *Fendler 51* at the Missouri Botanical Garden. Yet in spite of such lack of constancy the species seems to form an unit distinguishable from most other Ingas within its range (especially by the large, elongate corolla, the several pairs of leaflets, the wingless rachis, and the spicate inflorescence).

19. INGA COCLEENSIS Pittier, in Contr. U. S. Nat. Herb. 18:211. 1916.

Tree, the branchlets densely dark rubiginous-tomentose. Leaves large, 12-foliolate; petiole about 2.5 cm. long, terete, tomentose like the branchlets; rachis about 16 cm. long, unwinged, pubescent like the petiole, bearing above at insertion of the petiolules a large, sessile, oval, concave gland; leaflets 6 pairs, mostly elliptic-lanceolate, the terminal ones about 13 cm. long and 4 cm. wide, the basal pair somewhat smaller, rounded or obtuse basally, acute and somewhat acuminate apically, rather coarsely short-pubescent above except tomentose on the costa, tomentose below, the veins elevated below and slightly impressed above, reticulate; stipules not known. Inflorescence of axillary pedunculate spikes; peduncle 4–5 cm. long, tomentose like the branchlets; floriferous portion thick, about 4 cm. long, the bracts caducous. Flowers sessile; calyx tubular, 6–7 mm. long, rubiginous-pubescent; corolla not known. Legume (immature) slender, terete by thickening of the margins, longitudinally sulcate, ferruginous-tomentose, twisted.

Panama.

COCLÉ: Bismarck, *Williams 405*.

The species is known only from a broken fragment found on the ground, including one complete leaf and two or three immature fruits. A photograph of the type shows resemblance to the rather hazily defined *I. multijuga*, of which further collections may prove *I. cocleense* to be a synonym.

20. INGA RUIZIANA G. Don, Gen. Hist. Dichl. Pl. 2:391. 1832.

Inga fagifolia G. Don, loc. cit. 391. 1832, non Willd., fide Benth.
Inga foliosa Benth. in Hook. Jour. Bot. 4:597. 1845.
Feuillćea Ruiziana Ktze. Rev. Gen. Pl. 1:189. 1891.
Inga confusa Britt. & Rose, in N. Am. Fl. 23:5. 1928.

Tree to 20 or more m., the branchlets conspicuously lenticellate and ferruginous-puberulent towards the tip. Leaves large, even-pinnate, generally 12-foliolate; petioles 1–2 cm. long, terete or nearly so, ferruginous-puberulent, swollen basally; rachis about 15 cm. long, like the petiole except margined laterally above, bearing disc-like, sessile, generally depressed glands 1–2 mm. in diameter between insertion of the petiolules; leaflets usually 6 pairs, mostly elliptic, the uppermost often obovate-elliptic and up to 25 cm. long and 8 cm. broad, the lowermost usually only ⅓ or ¼ this size and somewhat ovate, short-acuminate apically, obtuse and somewhat inequilateral basally, the veins prominently reticulate and

Fig. 82. *Inga Ruiziana*

puberulent below, lightly indented above, the leaflet subglabrous and drying darker above; stipules caducous. Inflorescence terminal and subterminal, tomentulose, of 2–3 pedunculate spikes fasciculate from each of several nodes or axils, the spikes 3–4 cm. long, the floriferous portion ovate and about 1 cm. long. Flowers congested, white, subsessile; calyx subturbinate, 3–4 mm. long, contracted gradually baseward, densely puberulent; corolla 7–8 mm. long, strigose-puberulent; stamens many; filaments almost 2 cm. long, united below for at least half their length, the tube slightly exceeding the corolla; anthers minute. Legume reported 10–15 cm. long and 2–2.5 cm. wide, flat, rounded apically and basally, somewhat pubescent, the margins elevated.

Nicaragua to Peru and Brazil.

CANAL ZONE: Gamboa, *Pittier 6520;* Peluca Hydrographic Station, *Steyermark & Allen 17271;* Quebrada Salamanca, *Dodge, Steyermark & Allen s. n.* (1934). COLÓN: R. Fató, *Pittier 3917.* DARIÉN: Marraganti, *Williams 768;* Sambú River, *Pittier 5533.* BOCAS DEL TORO: Chiriquí Lagoon, *H. von Wedel 2012, 2677;* Water Valley, *H. von Wedel 844.*

Although the type of the species is unavailable for examination, various descriptions and keys are precise enough to indicate *I. confusa* Britt. & Rose as synonymous with *I. Ruiziana* G. Don. Certainly herbarium material of the two species appears identical.

21. INGA MICROSTACHYA Britt. & Killip, in Ann. N. Y. Acad. Sci. 35:115. 1936.

Unarmed tree, the branchlets fulvous-puberulent when very young, soon becoming glabrous or subglabrous, very pronouncedly raised white-lenticellate, somewhat flexuous, subangulate below the nodes because of decurrent ridges from the axils. Leaves large, the leaflets 4 or 5 pairs opposite on the rachis; petioles mostly 1–2 cm. long, terete except briefly ridged laterally, subglabrous or lightly puberulent; rachis up to 12 or more cm. long, unwinged but ridged laterally especially below the foliolar nodes, sulcate above, puberulent to subglabrous, bearing a prominent, sessile, cupulate gland at insertion of each pair of leaflets; leaflets mostly elliptic-lanceolate, up to 18 cm. long and 7 cm. wide in the larger (terminal) leaflets, the basal leaflets perhaps one-third as long and wide, acute-acuminate apically, inequilaterally acute or obtuse basally, glabrous and lustrous above, the venation visible but not as prominent as below, glabrous below except often puberulent on the main veins, the venation prominently reticulate; stipules linear, early caducous. Inflorescence of fasciculate clusters of pedunculate spikes from terminal (immaturely foliate) and subterminal axils; peduncles 2–5 cm. long, puberulent or tomentulose; spikes short, 1–2 cm. long, the floral bracts minute. Flowers sessile, moderately congested; calyx cupulate, slightly less than 2 mm. long, puberulent, the lobes irregular; corolla funnelform-cylindric, about 4 mm. long (in Panama), puberulent at least apically; staminal tube about equalling the corolla; ovary oblong, short, compressed, glabrous except for a few setae marginally. Legume not known, but presumably flat.

Panama and Colombia.

CANAL ZONE: Fort Sherman Military Reservation, *Maxon & Valentine 6979.*

This species, a new record for Panama, somewhat resembles both *I. Ruiziana* and *I. punctata* of that country, but it lacks the obovate terminal leaflets of the former and possesses more (4–5 pairs) leaflets than the latter (2–3 pairs). Its exact relationships with South American species such as *I. nobilis* Willd., *I. lenticellata* Benth., *I. Caldasiana* Britt. & Killip, and others which it resembles, awaits work of the monographer.

22. INGA ROUSSOVIANA Pittier, in Contr. U. S. Nat. Herb. 18:175. 1916.

Inga Schippii Standl. in Field Mus. Publ. Bot. 11:132. 1932.

Small tree, the branchlets ferruginous-lenticellate and puberulent towards the tips. Leaves moderately large, mostly 6-foliolate; petioles usually 1–2 cm. long although reported up to 4 cm. long, subterete, puberulent or subglabrous; rachis mostly about 7 cm. long but often longer or shorter, flattened and margined above, lightly ferruginous-puberulent to glabrous, bearing small, knob-like, concave glands between insertions of the petiolules (the glands variable in shape and size, infrequently suppressed); leaflets 2–4 (usually 3) pairs, generally oblong or elliptic, the uppermost somewhat obovate, up to 18 cm. long and 3–7 cm. wide, the lowermost only about ⅓ as large, broadly or narrowly cuneate basally, blunt to short-acuminate apically, glabrous except occasionally on veins below, the veins very prominent below, less so above; stipules reported ovate, about 5 mm. long, ferruginous-tomentose, caducous. Inflorescence a terminal or subterminal paniculate shoot, the peduncled umbels 1 to few from the defoliate nodes; the bracts and axis ferruginous-tomentose; peduncles 1–2 cm. long; flowers whitish, umbellate from the tip of the peduncle on prominent pedicels usually 4–5 mm. long. Flowers several in each umbel, whitish; calyx turbinate-subcampanulate, 3–6 mm. long, expanded upward, hirsute-tomentose; corolla about 9 mm. long, hirsute-villous without, the teeth about 2 mm. long; stamens about 18 mm. long, united below into a tube about 1 cm. long. Legume linear-oblong, up to 17 cm. long and 2.2 cm. wide, apiculate, rounded basally and stipitate, flat, ferruginous-tomentulose, prominently margined.

British Honduras and Guatemala to Panama; Colombia?

BOCAS DEL TORO: Changuinola Valley, *Stork 272; Cooper & Slater 13.* CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 270;* R. Chagres, *Steyermark & Allen 16781;* France Field, *Standley 30325.* CHIRIQUÍ: San Felix, *Pittier 5270.*

The Canal Zone specimens have smaller flowers and shorter pedicels than is usual for the species, and probably represent intergradation towards *I. Williamsii* Pittier, a species of doubtful specific distinction. *I. santanderensis* Britt. & Killip (in Ann. N. Y. Acad. Sci. 35:114), of Colombia, is probably nothing more than a robust form of *I. Roussoviana,* but having seen no specimens of the former other than the type I cannot pass judgment on the constancy of this difference. The type of *I. Schippii,* also with a more robust calyx than is typical of *I. Roussoviana,* is nevertheless linked by a series of intergrading specimens.

23. INGA WILLIAMSII Pittier, in Contr. U. S. Nat. Herb. 18:176. 1916.

Small tree, the branchlets ferruginous-lenticellate and puberulent towards the tips. Leaves moderate, mostly 6-foliolate; petioles about 2 cm. long, subterete, puberulent; rachis mostly 6 or 7 cm. long, puberulent like the petiole, flattened and margined above, bearing small glands between insertions of the leaflets or the glands partly or wholly suppressed; leaflets usually 3 pair, more or less elliptic, the upper-

most up to about 12 cm. long and 4 or 5 cm. wide, the lowermost only ¼ as large, subcuneate basally, acute to emarginate apically, glabrous except on the veins below, the veins very prominent below, not elevated above; stipules reported lanceolate, variable in size, caducous. Inflorescence a terminal or subterminal paniculate shoot or reduced to only 1 or a few pedunculate umbels from the defoliate nodes, ferruginous-tomentose; peduncles 1–2 cm. long; pedicels 1–2 mm. long, arising more or less in umbellate or subcapitate fashion from the tip of the peduncle. Flowers whitish; calyx about 4 mm. long, densely pubescent without; corolla short, typically 6 or 7 mm. long, villous-tomentose without; staminal tube scarcely exserted, the filaments about 15 mm. long. Legume linear-oblong, up to 10 cm. long, about 2 cm. wide, arcuate, flat but thick, densely ferruginous-tomentose when young.

Panama; Colombia?

CANAL ZONE: Barro Colorado Island, *Wetmore & Abbe 101; Bangham 512; Zetek 3920;* R. Chagres, *Dodge & Allen 17400.* COLÓN: Bismarck, *Williams 285.*

This species seems to differ from *I. Roussoviana* almost solely in having notably shorter pedicels, and it probably should constitute but a variety of that species. We hesitate, however, to make this reduction until accumulation of more material can prove the frequency of intergradation. *I. Mutisii* Britt. & Killip (Ann. N. Y. Acad. Sci. 35:114) of Colombia, with leaflets up to 22 cm. long, is apparently just a more robust form of *I. Williamsii.*

24. INGA **gigantifoliola** Schery, sp. nov.

Arbor ramulis glabris lenticellatis; foliis permagnis plerumque 3-jugatis, petiolis aliquanto elongatis ca. 8 cm. longis teretibus exalatis glabris, rhachibus elongatis ad 20 cm. longis, exalatis, glandulam interfoliolarem disciformem sessilem, ornatis; petiolulis ca. 5 mm. longis; foliolis ovato-ellipticis ellipticisve, 13–40 cm. longis, 7–14 cm. latis, abrupte angustatis acuminatisque, basi late subcuneatis, stipulis non visis; inflorescentia spicibus tenuibus 1 vel paucibus ex axi, parte pedunculari ca 5 mm. longo, parte florifero ca. 5 mm. longo, bracteis minutis; floribus subsessilibus albis; calyce tubulati-cupuliformi, ad 2.5 mm. longo, glabro, estriato apice undulato; corolla tubulati-infundibuliformi, ad 9 mm. longa, subglabra; staminibus ad 2 cm. longis, tubo aliquanto exserto; ovario glabro, multiovulato; leguminibus verisimiliter planis glabris.

Small or moderate tree, more or less glabrous throughout, the branchlets lenticellate. Leaves very large, 6- (sometimes 4?-) foliolate; petiole elongate, almost 8 cm. long, terete and unwinged, lenticellate, glabrous, callous at the extreme base; rachis up to 20 cm. long, terete and unwinged like the petiole, bearing an inconspicuous, flat, sessile gland between insertion of the petiolules; petiolules about 5 mm. long, callous, glabrous; leaflets mostly 3 pairs, elliptic or ovate-elliptic, 13–40 cm. long and 7–14 cm. wide, rather abruptly narrowed apically into an acumen 1–2 cm. long, similarly contracted basally into a short subcuneate base, completely glabrous, the veins somewhat impressed above and elevated below, chartaceous;

Fig. 83. *Inga gigantifolia*

stipules not present. Inflorescence 1 to few, of very short, axillary, pedunculate spikes (sometimes borne on older, defoliate branches?), the peduncular portion about 5 mm. long and lightly puberulent, the floriferous portion about 5 mm. long also; bracts triangular-lanceolate, minute. Flowers small, white, scarcely pedicellate; calyx tubular-cupular, about 2.0–2.5 mm. long, subglabrous without, not striate, sometimes cleft to one side but otherwise the teeth broader than tall and the rim

appearing more or less undulate; corolla funnelform-tubular, 8–9 mm. long, subglabrous, the lobes 1–2 mm. long; stamens up to 2 cm. long, the staminal tube briefly exserted; ovary turgid-quadrangular, glabrous, multiovulate. Legume not known in type specimen, probably linear-oblong, flat, glabrous, the margins little thickened.

Panama; South America?

BOCAS DEL TORO: Fish Creek Mts., *H. von Wedel 2349* (Herb. Missouri Bot. Gard., TYPE).

The species would fall into the section BOURGONIA of the genus as interpreted by Pittier following Bentham. It is quite distinctive from most species in the extremely large leaflet size.

The type specimen appears identical in many respects with the Amazonian (Río Solimoes) 7th Krukoff Expedition specimens, *Krukoff 8215* and *8228*. The Krukoff material in flower *(8215)* and fruit *(8228)* was found undetermined in the herbarium; the flowers were of slightly smaller dimensions, pronouncedly more pedicellate, and the calyx slightly more elongate than in the Panamanian material. Nevertheless, similarity in leaflet, inflorescence and floral structure would seem to indicate that the Krukoff material has close affinities with the Panamanian specimen. In any event the Amazonian material supports the belief that, in spite of the separation of the inflorescence from the leaves in the H. von Wedel specimen, flower and branch are both from the same plant; and that similarity in ovary structure between *H. von Wedel 2349* and *Krukoff 8215* may indicate that the fruit of the Panamanian specimen would at least somewhat resemble that of *Krukoff 8228*.

25. INGA PUNCTATA Willd. Sp. Pl. 4:1016. 1806.

Mimosa sericea Poir. in Lam. Encycl. Meth. Suppl. 1:42. 1810.
Inga leptoloba Schlecht. in Linnaea 12:560. 1838.
Inga punctata var. *panamensis* Benth. in Trans. Linn. Soc. 30:613. 1875.
Feuilléea punctata Ktze. Rev. Gen. Pl. 1:188. 1891.
Inga punctata chagrensis Pittier, in Jour. Dept. Agr. Porto Rica 13:135. 1929.

Small or moderate tree to 15 m., the branchlets strigose-puberulent and markedly lenticellate. Leaves moderately large, pinnate, 4- to 6-foliolate; petioles 2–4 cm. long, terete or nearly so, puberulent like the branchlets, swollen-callous basally; rachis similar to and (the internodes) about as long as or slightly longer than the petiole, wingless, bearing disc-like or subconic glands between insertions of the petiolules (or these glands in part or entirely suppressed in some specimens); leaflets 2 or 3 pairs, elliptic to ovate, acuminate, those of the apical pair larger, up to 20 cm. long and 9 cm. wide, those of the lowermost pair usually about half as long and broad, strigose-puberulent on both surfaces; stipules linear-lanceolate, 3–4 mm. long, caducous. Inflorescence an axillary, subterminal, paniculate or corymbiform branch, the secondary spicate peduncles umbellate from the nodes, or sometimes the spikes fasciculate or simple-umbellate directly from the axil; spikes short, the floriferous portion scarcely more than 1 cm. long, the many flowers densely

congested. Flowers sessile, whitish; calyx subturbinate, 3–5 mm. long, the 5 teeth conspicuous but only about 0.5 mm. long, puberulent without; corolla tubular, somewhat expanded above the calyx, 7–9 mm. long, the lobes about 1 mm. long, pubescent without; stamens many, the filaments almost 2 cm. long in age, united into a tube for about ½ their length, glabrous, the anthers minute, bilocular, only a fraction of a mm. long; ovary and style glabrous. Legume linear-oblong, about 13 cm. long and 2.5 cm. wide, slightly arcuate, lightly pubescent, flattened, somewhat margined, apparently indehiscent.

Mexico and Central America to the Amazon Valley and Peru; Tobago.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 73;* Chiriquí Lagoon, *H. von Wedel 1069, 1230, 2357, 2387.* CANAL ZONE: Barro Colorado Island, *Zetek 3837, 3847, 3867;* "Chagres," *Fendler 89;* R. Chagres, *Steyermark & Allen 16778;* Gatún, *Goldman 1865; Hayes 55.* CHIRIQUÍ: Boquete, *Davidson 814.* COCLÉ: El Valle de Antón, *Allen 3700.* COLÓN: R. Culebra, *Pittier 4161.* DARIÉN: El Real, *Allen 966;* Pinogana, *Allen 4281.* PANAMÁ: Chepo, *Hunter & Allen 95.* VERAGUAS: near Soná, *Woodson, Seibert & Allen 486.*

Inga leptoloba has been retained as a species distinct from *I. punctata* by most authors (Bentham, Britton & Rose, etc.), and Standley (Flora Guatemala) lists it as doubtfully distinct. Bentham's distinction between *I. leptoloba* and *I. punctata* is not clear, while Britton & Rose and Standley separate the two species on the basis of bifoliolate leaves in the latter vs. trifoliolate leaves in the former. However, many specimens occur with both bi- and tri-foliolate leaves on the same plant, and no supporting or correlating characters are apparent to strengthen this demarcation. Both bi- and tri-foliolate specimens exhibit the same range of variability in rachial gland structure, flower size, and type of inflorescence, and none of the vegetative distinctions mentioned by Pittier (Contr. U. S. Nat. Herb. 18:187) exhibit constancy when large numbers of specimens are examined. Thus it seems most practical to unite these two names as a single species, or at least reduce *I. leptoloba* to varietal status under *I. punctata.*

26. INGA LAURINA (Sw.) Willd. Sp. Pl. 4:1018. 1806.

Mimosa fagifolia Jacq. Stirp. Amer. Hist. 1:264, *t. 164.* 1763, non L., fide Benth.
Mimosa laurina Sw. Prodr. Veg. Ind. Occ. 85. 1788.
Feuilléea laurina Ktze. Rev. Gen. Pl. 1:184. 1891.

Moderate-sized tree, the branchlets glabrous and markedly lenticellate. Leaves moderate-sized, usually 4- (or sometimes 6-, or reported occasionally 2-) foliolate; petiole 1–2 cm. long, terete except angled laterally above, glabrous; rachis 2–5 cm. long, glabrous, wingless but ridged and somewhat marginate laterally above, bearing a small, sessile, disc-like or subcupuliform gland between insertion of the petiolules; leaflets usually 2 pairs, sometimes 3 or 1? pair, mostly oblong or elliptic, 4–12 cm. long and 1.5–5.5 cm. wide, usually acute and bluntly acuminate apically, cuneate and slightly inequilateral basally, glabrous above and below; stipules linear-oblong, up to 5 or 6 mm. long, pubescent, subpersistent or caducous. Inflorescence of 1 or 2 elongate spikes from each of a number of foliate or defoliate axils; spikes

subglabrous, about 10 cm. long, the peduncular portion only about 2 cm. long, the many flowers scattered over the remaining floriferous portion. Flowers whitish, glabrous to puberulent; calyx cupuliform-tubular, 1–2 mm. long, the teeth minute but distinct; corolla usually 4–5 mm. long, narrowed basally, expanded apically, subglabrous; stamens 12–15 mm. long, fused basally into a tube greatly and noticeably exceeding the corolla (Panama?) or only slightly exceeding the corolla. Legume reported flat and strongly compressed, 7–15 cm. long and 2–3.5 cm. wide, subglabrous, the margins thickened.

Mexico to Panama; West Indies.

CANAL ZONE: Barro Colorado Island, *Bangham 547*. CHIRIQUÍ: Boca Chica, *Pittier 5119*. COCLÉ: Bismarck, *Williams 532*. HERRERA: Ocu, *Allen 4037*. PANAMÁ: Capira, *Allen 1688*; R. Pacora, *Allen 817*.

As with most species of the genus, *I. laurina* exhibits variability, noticeable here especially in length of the staminal tube relative to the corolla. In fact, certain specimens are almost identical with respect to the elongate staminal tube to South American material generally accepted as *I. fagifolia* Willd. Bentham (Trans. Linn. Soc. 30:608) considered the elongate staminal tube, along with a more pronouncedly bordered rachis and a fruit difference, as distinguishing *I. fagifolia* from *I. laurina*. Panamanian (and Mexican) material could sometimes be considered either of these two species, leading us to believe that combining these names (and probably that of *I. cylindrica* (Vell.) Mart. also) might eventually prove in order. In Panama, *I. laurina* (regarding *I. fagifolia* as a separate species not occurring there) is fairly readily delimited from other species except *I. marginata* by distinctive leaflet appearance and the elongate, relatively lax spikes. *I. coruscans* H. & B. ex Willd., of northern South America, resembles *I. laurina* except for the leaflet which is like that of *I. marginata*.

27. INGA CALDASIANA Britt. & Killip, in Ann. N. Y. Acad. Sci. 35:115. 1936.

Forest tree to 20 m., the branchlets glabrous or subglabrous, prominently lenticellate, the lenticels and bark reddish-brown. Leaves large, normally 6-foliolate, the basal pair of leaflets sometimes caducous, occasionally only one member of the terminal pair present; petiole short, at most 1.5 cm. long, the lower portion swollen and callous, glabrous or sparsely puberulent above; rachis usually 6–8 cm. long, unwinged but frequently slightly marginate below the apical leaflets and somewhat angled above, subglabrous, bearing between insertion of the petiolules a sessile, patelliform gland about 1 mm. in diameter; leaflets elliptic or nearly so, about 15 cm. long and 6–7 cm. wide, the basal leaflets somewhat smaller, abruptly narrowed and short-acuminate apically, cuneate or subcuneate basally, glabrous except perhaps minutely puberulous on the costa; petiolules 2–3 mm. long, callous, puberulous; stipules linear-oblong, usually 8–12 mm. long, puberulous. Inflorescence of 1 to few axillary, short-pedunculate spikes, the peduncular portion less than 2 cm. long, the floriferous portion puberulent and as much as 10 cm. long but usually about 6 cm. long; bracts subtending the flowers minute, sublinear and ascending-expanded apically. Flowers moderately lax, sessile, white; calyx cupular,

less than 1 mm. long, puberulent; corolla tubular-funnelform, about 4 mm. long, subglabrous except canescent-puberulent at tips of the lobes; stamens 1 cm. long or slightly longer, the staminal tube exserted 2–3 mm. beyond the corolla; ovary oblong, compressed, glabrous; style truncate, exserted beyond the stamens. Legume not known.

Colombia and eastern Panama.

DARIÉN: Yavisa, *Allen 4585*.

The Panamanian specimen cited matches fairly well the type of *I. Caldasiana*, and as this species it constitutes a new record for Panama. *Lawrance 784* from Boyaca, Colombia, is probably likewise *I. Caldasiana* and not *I. marginata* as found labeled in the herbarium. The inflorescence and flowers of *I. Caldasiana* might well be *I. marginata* or *I. laurina*, but it is hard to reconcile the leaf with either of these species. The unwinged, scarcely marginate leaf rachis and large leaflet size are unlike *I. marginata*, and the much larger leaflet and large stipule-like bracts are unlike *I. laurina*. Also similar to *I. Caldasiana* are the South American species *I. Klugii* Standl. ex Macbride and *I. Bourgoni* (Aubl.) DC.

28. INGA MARGINATA Willd. Sp. Pl. 4:1015. 1806.

?Inga sapida HBK. Nov. Gen. & Sp. 6:286. 1824.
Mimosa semialata Vell. Fl. Flum. Ic. 11:*t. 5*. 1827.
Inga guayaquilensis G. Don, Gen. Hist. Dichl. Pl. 2:391. 1832, fide Benth.
Inga odorata G. Don, loc. cit. 388. 1832, ex char. fide Benth.
Inga excelsa Poepp. & Endl. Nov. Gen. & Sp. 3:78. 1845, fide Benth.
Inga puberula Benth. in Hook. Lond. Jour. Bot. 4:589. 1845.
Inga pycnostachya Benth. loc. cit. 1845.
Feuilléea marginata Ktze. Rev. Gen. Pl. 1:188. 1891.

Moderate-sized tree to 10 or 15 m., the branchlets glabrous, lenticellate. Leaves moderate, 4-foliolate; petiole short, usually about 1 cm. long, marginate or alate apically, terete and callous basally; rachis 2–4 cm. long, usually prominently alate, the wing broadest apically, bearing a sessile, patelliform gland between insertion of the petiolules; leaflets 2 pairs, narrowly elliptic or elliptic-lanceolate, sharply acuminate apically, cuneate and somewhat inequilateral basally, the terminal pair up to 15 cm. long and 2–5 cm. wide, the basal pair about ⅔ as large, essentially glabrous above and below; stipules linear, about 5 mm. long, caducous. Inflorescence of 1 to few spikes from the leaf axils, the spikes up to 10 cm. long and laxly floriferous for all except the lower several mm., glabrous or lightly puberulent. Flowers sessile, whitish; calyx campanulate or short-tubular, scarcely more than 1 mm. long, somewhat puberulent, the teeth prominent; corolla subfunnelform, 3–4 mm. long, gradually constricted basally, essentially glabrous; stamens about 12 mm. long, the staminal tube exserted 1–2 mm. beyond the corolla. Legume up to 12 cm. long and 1.5 cm. wide, flat, thickened about the seeds, lightly margined.

Costa Rica, Panama, northern South America.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 282;* Chiriquí Lagoon, *H. von Wedel 1378, 1549, 1807*. CANAL ZONE: Barro Colorado Island, *Zetek z4322;* Gatún Valley, *Pittier 6512*. COCLÉ: El Valle, *Allen 2231*. DARIÉN: Sambú River, *Pittier 5579*.

Fig. 84. *Inga marginata*

SPECIMENS OF UNCERTAIN STATUS

The *Allen 17282* (Canal Zone: R. Pequení), in very young bud, lacking both fruit and corolla, had been filed in the Missouri Botanical Garden herbarium as *Inga panamensis* Seem. Such determination would seem decidedly incorrect. In Pittier's treatment of *Inga* (Jour. Dept. Agr. Porto Rico 13. 1929) the plant would likely fall into section LEPTINGA, with affinities near *I. portobellensis* Beurling, and may be that species. However, accurate comparisons cannot be made because of the incompleteness of the specimen, and its exact status must remain in doubt.

Two sterile specimens labeled *Inga edulis*, collected by James Zetek (*No. 3907* from Barro Colorado Island, and *No. 3927* from near Chorrera, Panamá), appear different, as judged by leaf alone, from any species listed from Panama. It is impossible to give an exact determination to such sterile material, and unless dupli-

cates occur showing floral characters the specimens mentioned will have to remain indecisively located as to species.

NAMES OF UNCERTAIN APPLICATION, POSSIBLY EMBRACING PANAMANIAN SPECIES

INGA LINDENIANA Benth. in Hook. Lond. Jour. Bot. 4:608. 1845.

This species has been restricted by Pittier and Britton and Rose to the type, from Teapa, Mexico. Bentham, however, had considered *I. mucuna* a synonym of this name and the species to be represented in Panama by Fendler and Duchassaing specimens. We have not had opportunity to examine either the type or these specimens.

INGA VERA Willd. Sp. Pl. 4:1010. 1806.

Inga Inga Britton, Fl. Burmuda, 170. 1918.

This species has apparently been thoroughly confused with *I. spuria* and related species. Bentham regarded *I. pauciflora* as synonymous with *I. vera,* with a distribution of the species in the West Indies, Central America and northern South America. Pittier later considered *I. vera* confined to the West Indies, and reestablished *I. pauciflora* as a continental species. Recent floras of Colombia, Costa Rica, and Guatemala fail to list *I. vera:* hence we include *I. pauciflora* but not *I. vera* as occurring in Panama (see discussion of *I. pauciflora*).

2. PITHECOLOBIUM[1] Martius

PITHECOLOBIUM Mart. Hort. Reg. Monac. 188. 1829, as *Pithecellobium* nom. conserv.

Zygia P. Browne, Nat. Hist. Jamaica, 279, *t. 22, f. 3.* 1756.
Spiroloba Raf. Sylva Tellur. 119. 1838.
Cathormion Hassk. Retzia, 231. 1855.
Feuilléea Ktze. Rev. Gen. 1:182. 1891, in part.
Siderocarpus Small, in Bull. N. Y. Bot. Gard. 2:91. 1901, homonym.
Havardia Small, loc. cit. 1901.
Samanea Merrill, in Jour. Wash. Acad. 6:46. 1916.
Abarema Pittier, in Trab. Mus. Com. Venezuela 2:86. 1927.
Jupunba Britt. & Rose, in N. Am. Fl. 23:24. 1928.
Punjuba Britt. & Rose, loc. cit. 28. 1928.
Cojoba Britt. & Rose, loc. cit. 29. 1928.
Ebenopsis Britt. & Rose, loc. cit. 33. 1928.
Painteria Britt. & Rose, loc. cit. 1928.
Chloroleucon Britt. & Rose, loc. cit. 36. 1928.
Pseudosamanea Harms, in Bot. Gart. Berlin Notizbl. 11:54. 1930.
Arthrosamanea Britt. & Rose, in Ann. N. Y. Acad. Sci. 35:128. 1936.
Macrosamanea Britt. & Rose, loc. cit. 131. 1936.

[1]The genus is written *Pithecellobium*, *Pithecollobium* or *Pithecolobium*. The spelling *Pithecolobium*, although lacking priority, has been followed by most authors, including Bentham, Engler & Gilg, Index Kew., Standley, Ducke, Macbride and many others. Pittier and a few others have followed Martius' later alteration of the original spelling, *Pithecollobium*. Merrill and Britton & Rose have used the original spelling *Pithecellobium,* and the genus has been so listed in the conserved name list of the International Rules of Botanical Nomenclature. On the basis of general acceptance and simplicity we follow here the spelling *Pithecolobium*.

Trees or shrubs, unarmed or, less frequently, armed with stipular spines or thorns, the branchlets usually puberulent or tomentulose and lenticellate. Leaves small or large, except in very few species *("Cojoba")* bipinnate, the pinnae 1 to several pairs opposite on the rachis; leaflets 1 to many pairs opposite on the pinnular rachis (except frequently basal pair alternate or one leaflet of pair aborted); petiole unwinged, usually short, rarely bearing a gland on the upper side; rachis similar to the petiole, generally bearing a gland at insertion of each pair of pinnae; pinnular rachis usually similarly glandular, the glands commonly cupulate; leaflets 2 to many per pinna, small or large, entire, usually inequilateral, seldom heavily pubescent above; stipules minute or of prominent spines or thorns. Inflorescence of 1 to several axillary or supra-axillary, lateral or subterminal, pedunculate (rarely sessile) heads or spikes; floral bracts minute or conspicuous. Flowers pentamerous, sessile or rarely pedicellate, almost invariably whitish; calyx campanulate to tubular, pubescent or subglabrous, valvate, shallowly dentate; corolla tubular to funnelform, generally elongate, valvate, frequently tomentulose on the 5 lobes; stamens many, united below into a staminal tube included in or exceeding the corolla; ovary glabrous or pubescent, sessile or stipitate. Legume moniliform, compressed or flat, subcircinate, arcuate or almost straight, normally dehiscent, the valves often twisting after dehiscence; seeds often imbedded in pulp.

Tropics and subtropics of New World; one section (CLYPEARIA of Benth.) Far Eastern.

This predominantly New World genus exhibits great variability and has been a temptation to authors favoring segregation. A few of the segregate genera, for example, *Samanea* Merrill (Jour. Wash. Acad. 6:46. 1916), have little in common with *Pithecolobium* in general, and offer a case for establishment of separate (usually monotypic) genera. In the case of *Samanea,* Merrill argues his point well and convincingly, but fails to consider the results were each equally divergent species or grouping of species so accorded separate recognition. It is difficult enough to attempt to distinguish *Pithecolobium* from long-established genera of the MIMOSOIDEAE, such as *Calliandra, Albizzia,* etc., without adding confusion in the form of numerous segregates such as Britton and Rose have proposed. It is often nearly impossible to find into which of such segregate genera a species falls, and the key to these genera is impossible to work.

Unfortunately, segregations of even universally recognized genera in the MIMOSOIDEAE have been made chiefly on the basis of legume characters. Many specimens, of course, are not in fruit, and such specimens often resemble one genus as much as another. Thus determination often becomes a hit-or-miss matching of specimens. I am led to wonder whether legume characters would not have failed in many generic delimitations had sufficient fruiting specimens been on hand to exhibit variability and degrees of intergradation. Certainly, in Panama, consideration of *Pithecolobium* in a broad sense brings together in one "pigeon-hole" many diverse species which can then be comparatively easily keyed out on vegetative and floral characters.

a. Leaves once-pinnate; legume moniliform (*"Cojoba"*, in part).
  b. Floral bracts minute, not exserted nor readily visible in young head; costa and rachis glabrous or becoming glabrous in age; rachial glands mostly longitudinal ..... 1. P. MEMBRANACEUM
  bb. Floral bracts 2–6 mm. long, exserted beyond or visible among buds of young head; costa and rachis pubescent except subglabrous in *P. rufescens* var. *vallense;* rachial glands essentially isodiametric.
    c. Leaflets 1–5 pairs, only slightly asymmetrical, 2–15 cm. long (if small usually subglabrous on costa).
      d. Terminal pair of leaflets usually 10 cm. long or longer; costa of leaflet markedly pubescent below; floral bracts about 4 mm. long, exserted, the young head appearing burr-like ..... 2. P. RUFESCENS
      dd. Terminal pair of leaflets seldom as much as 7 cm. long; costa of leaflet subglabrous below; floral bracts less than 3 mm. long, comparatively inconspicuous in young head ..... 2a. P. RUFESCENS VAR. VALLENSE
    cc. Leaflets 4–8 pairs, markedly oblique or inequilateral basally, 2–6 cm. long, tomentose on the costa ..... 3. P. TUBULIFERUM
aa. Leaves bipinnate; legume various, seldom moniliform.
  b. Pinnae only 1 pair.
    c. Leaflets 3–12 per pinna; stems unarmed.
      d. Leaflets in pairs (even-pinnate); peduncle conspicuous, 2–24 cm. long; corolla elongate, 12–16 mm. long; legume moniliform.
        e. Leaflets 2–5 (usually 3) pairs per pinna; peduncle usually 2–3 but never more than 6 or 7 cm. long; corolla about 12 mm. long ..... 4. P. VALERIOI
        ee. Leaflets 4–6 pairs per pinna; peduncle 8–24 cm. long; corolla about 16 mm. long ..... 5. P. CATENATUM
      dd. Leaflets usually 3 or 5 (odd-pinnate) per pinna; heads or spikes scarcely pedunculate; corolla mostly 6–7 mm. long; legume flattened, of essentially uniform width *("Zygia")*.
        e. Leaflets 3 or 5 per pinna, broadly elliptic (normally less than 3 times as long as broad); flowers in nearly sessile, very condensed spikes or heads ..... 6. P. LATIFOLIUM
        ee. Leaflets 3 per pinna, narrowly elliptic (3 or more times as long as broad); flowers in short, lax spikes ..... 7. P. LONGIFOLIUM
    cc. Pinnae bifoliolate; stems normally armed with stipular spines.
      d. Flowers in pronounced spikes, the floriferous portion mostly 3–12 cm. long; corolla 4–11 mm. long; legume arcuate or twisting.
        e. Corolla 7–11 mm. long, stamens 4–6 cm. long ..... 8. P. HYMENEAEFOLIUM
        ee. Corolla 4–6 mm. long, stamens no more than 2.5 cm. long ..... 9. P. LANCEOLATUM
      dd. Flowers capitate or short-spicate, the floriferous portion never more than 2 cm. long; corolla 2–4 mm. long; legume coiled or subcircinate.
        e. Flowers in short spikes; inflorescence an expanded, branched panicle, the peduncles mostly 1–3 cm. long ..... 10. P. OBLONGUM
        ee. Flowers capitate; inflorescence a contracted panicle, the heads subsessile or on short peduncles less than 2 cm. long ..... 11. P. DULCE
  bb. Pinnae 2 to several pairs.
    c. Petiole bearing 1–3 sessile glands well below insertion of and not associated with the lowest pair of pinnae (or their scars); leaflets less than 10 mm. long.
      d. Commonly armed at some or most nodes with stipular spines; buds large, ovoid, with prominent bud scales; legume arcuate, the valves not coiling after dehiscence: *("Chloroleucon")* ..... 12. P. MANGENSE
      dd. Unarmed; buds slender, naked; legume circinate, twisting in dehiscence, or unknown.
        e. Leaflets about 40 pairs per pinna, glabrous, narrower (up to 2 mm. wide) ..... 13. P. PSEUDO-TAMARINDUS
        ee. Leaflets up to 16 pairs per pinna, pubescent below, broader (3–6 mm. wide) ..... 14. P. BARBOURIANUM
    cc. Petiole glandular at extreme apex only (if apparently glandular lower down, gland bordered by scars of aborted pinnae); leaflets 10 mm. long or longer.

d. Leaflets 10–25 mm. long; flowers sessile; legume moniliform-subterete, the valves twisting after dehiscence *("Cojoba")*, or unknown.
  e. Leaflets pubescent below, obtuse or rounded apically; flowers short (about 4 mm.? long), hirsutulous..... 14. P. BARBOURIANUM
  ee. Leaflets essentially glabrous, more or less acute apically; flowers elongate (about 1 cm. long), glabrous or nearly so..... 15. P. COSTARICENSE
dd. Leaflets 20–50 mm. long; flowers pedicellate; legume thickish but flat, uniform, the valves never twisting *("Samanea")*.
  e. Cupular gland between insertions of basal pinnae large, as much as 1 cm. long; leaflets and flowers lightly pubescent.... 16. P. MACRADENIUM
  ee. Gland at insertion of basal pinnae small or nearly obsolete; leaflets and flowers densely pubescent..... 17. P. SAMAN

1. PITHECOLOBIUM membranaceum (Benth.) Schery, comb. nov.

Inga membranacea Benth. in Trans. Linn. Soc. 30:606. 1875.
Cojoba glabra Britt. & Rose, in N. Am. Fl. 23:33. 1928.
Pithecolobium glabrum Standl. in Trop. Woods 34:40. 1933.
Pithecolobium Davidsoniae Standl. in Field Mus. Publ. Bot. 22:82. 1940.

Fig. 85. *Pithecolobium membranaceum*

Small or moderate tree, the branchlets rufous-tomentellous when very young, soon glabrate, lenticellate. Leaves moderate, once-pinnate, the leaflets 2–4 pairs; petiole 1–3 cm. long, puberulent becoming glabrate, terete, bearing a sessile, concave, longitudinally extended gland shortly below insertion of basal pair of leaflets; rachis similar, 2–7 cm. long, bearing similar glands just below insertion of each pair of leaflets; leaflets elliptic, 3–11 (mostly 6–7) cm. long and usually about 3 cm. wide, briefly contracted apically into a bluntly acute tip, cuneate or subcuneate basally, glabrous above and below, finely and noticeably reticulate below;

stipules caducous or lacking in specimens examined. Inflorescence an axillary, pedunculate head; peduncle about 3 cm. long, puberulent, bearing a small bract (often caducous) on the upper half; head dense, subumbellate, the subtending bracts minute, rufous. Flowers sessile, greenish-white or pale greenish-yellow; calyx campanulate or campanulate-subtubular, 1–2 mm. long, glabrous except rufous-tomentose on the teeth; corolla tubular-funnelform, about 6 mm. long, glabrous except minutely puberulent on the teeth; stamens about 1 cm. long, the staminal tube included; ovary glabrous, sessile. Legume 2–10 cm. long, terete and moniliform, stipitate, red?, the valves twisting after dehiscence.

Costa Rica and western Panama.

CHIRIQUÍ: Boquete, *Seemann 1192;* Callejón Seco, *Woodson & Schery 490; Davidson 770;* Casita Alta, *Woodson, Allen & Seibert 864;* Camiseta, *M. E. (Davidson) Terry 1352;* R. Chiriquí Viejo, *G. White 61; P. White 335;* Volcan de Chiriquí, *Davidson 900;* Quebrado Velo, *Woodson & Schery 272.*

The species somewhat resembles *P. rufescens,* and grades into it, but as a rule has a more delicate, membranous leaflet and lacks the elongate subtending floral bracts so conspicuous in the (immature) head of *P. rufescens.* It belongs to the "*Cojoba*" section of *Pithecolobium,* and is distinguished from all except 2 species of that genus (in Panama) by the once-pinnate leaves and the peculiar moniliform legume.

The type of this species *(Inga membranacea, Seemann 1192)* has not been examined, but judging from a photograph of it in the U. S. Nat. Herbarium there seems little doubt but that it belongs with the other once-pinnate Pithecolobiums which Pittier transferred from *Inga,* and that the newer *Pithecolobium* species listed above can be referred to it. The species has rested as *Inga* since original publication without a second collection having been recognized.

2. PITHECOLOBIUM RUFESCENS (Benth.) Pittier, in Contr. U. S. Nat. Herb. 18:181. 1916.

Inga rufescens Benth. in Hook. Lond. Jour. Bot. 4:585. 1845.
Inga globulifera Benth. loc. cit. 1845, fide Pittier.
Inga Billbergiana Benth. loc. cit. 1845, fide Pittier.
Feuilléea rufescens Ktze. Rev. Gen. Pl. 1:189. 1891.
Cojoba rufescens Britt. & Rose, in N. Am. Fl. 23:32. 1928.

Tree, up to several meters tall, the branchlets ferruginous-tomentulose and usually prominently lenticellate. Leaves moderate or moderately large, once-pinnate, the leaflets 1–5 (mostly 3–4) pairs; petiole short, normally 1 cm. or less long, pubescent; rachis up to 10 cm. long, pubescent, subsulcate above, bearing a sessile, concave gland at insertion of leaflet pairs; leaflets mostly oblong, 4–15 cm. long and 2–6 cm. wide, rounded to bluntly acute-acuminate apically, subcuneate to rounded basally, very slightly inequilateral, usually glabrous above, lightly pubescent below except the costa rather heavily so, the lateral veins prominent and elevated below; stipules linear, early caducous. Inflorescence of solitary or geminate pedunculate heads from subterminal axils; peduncle 1–5 (usually about 2) cm.

Fig. 86. *Pithecolobium rufescens*

long, rufous-pubescent, generally bearing a solitary bract above the middle; head condensed; floral bracts linear, about 4 mm. long, ciliate, giving the head prior to anthesis a burr-like appearance. Flowers sessile, white; calyx short-tubular, about 2 mm. long, rufous-pubescent apically; corolla tubular-funnelform, 6 or 7 mm. long, rufous-pubescent on the lobes; stamens about 15 mm. long, the staminal tube included; ovary sessile, puberulent apically. Legume linear-moniliform, up to 15 cm. long, reddish with black seeds, puberulent, the valves very twisted after dehiscence.

Panama and Colombia.

CANAL ZONE: Ancón, *Pittier 2747*; Barro Colorado Island, *Woodworth & Vestal 677*; *Kenoyer 369*; Miraflores, *Allen 1749, 1759*; *G. White 152*; Pueblo Nuevo, *P. White 303*; R. Indio Hydrographic Station, *Steyermark 17419*. COCLÉ: Santa Clara, *Muenscher 16241, 16293*. COLÓN: Porto Bello, *Pittier 2490*. PANAMÁ: Chepo, *Dodge, Hunter, Steyermark & Allen 16626*; *Pittier 4493*; San José Island, *Erlanson 39, 368*; Taboga Island, *Standley 27943*.

This species exhibits considerable variability, and observation of material at hand supports belief that Pittier was entirely correct in reducing to synonymy Bentham's *I. globulifera* and *I. Billbergiana.* Likewise, Pittier's transfer of this and related species from *Inga* to *Pithecolobium* seems justified for the reasons he gives, although from the standpoint of practical identification the species could be more easily located in *Inga,* by means of the once-pinnate leaf criterion established by Bentham. As now recognized by most authors these few species of *Pithecolobium* ("*Cojoba*" of Britt. & Rose) are the only species of the MIMOSOIDEAE aside from *Inga* with once-pinnate leaves. Unfortunately rejection from *Inga* and inclusion in the "catch-all" *Pithecolobium* involves chiefly legume characters (moniliform fruit not found in *Inga*) not to be had in the majority of specimens. The legume resembles that of most species of *Pithecolobium* little more than the legume in *Inga,* and on this basis there may be some justification for Britton and Rose's genus *Cojoba.*

2a. PITHECOLOBIUM RUFESCENS (Benth.) Pittier var. **vallense** Schery, var. nov.

Arbor ramulis inconspicue lenticellatis, foliolis specie minoribus subglabris; bracteis capitulorum speciei similibus sed minoribus.

Tree of medium height, the branchlets rufous-tomentulose when very young, glabrate in age, inconspicuously lenticellate. Leaves small, once-pinnate, the leaflets 3–5 pairs; petioles very short, usually less than 5 mm. long, terete, puberulent; rachis up to 5 cm. long, like the petiole, bearing a sessile, concave gland just below insertion of the pairs of leaflets; leaflets oblong to narrowly elliptic, usually not longer than 6 cm., nearly glabrous, mostly obtuse apically and basally. Inflorescence an axillary, pedunculate head; floral bracts similar to those of the species but somewhat smaller and perhaps intermediate to condition found in *P. membranaceum.* Flowers white, sessile; calyx campanulate, little over 1 mm. long, pubescent apically; corolla tubular-funnelform, about 6 mm. long, pubescent on the lobes. Legume moniliform, red, the seeds black.

Apparently found only in vicinity of El Valle de Antón, Coclé, Panama.

COCLÉ: El Valle, *Allen 770* (Herb. Missouri Bot. Gard., TYPE), *1834* (COTYPE), *2495; Hunter & Allen 355.*

This entity has been described as a variety rather than as a species in that degrees of intermediacy (*Hunter & Allen 355* especially) occur towards *P. rufescens.* Its geographic distribution, as far as known, fits nicely the concept of a localized variety.

3. PITHECOLOBIUM TUBULIFERUM Pittier, in Contr. U. S. Nat. Herb. 18:181. 1916.

Inga tubulifera Benth. in Hook. Lond. Jour. Bot. 4:584. 1845.
Cojoba tubulifera Britt. & Rose, in N. Am. Fl. 23:32. 1928.

Shrub or small tree, the young branchlets brownish tomentose, becoming subglabrous in age and inconspicuously lenticellate. Leaves moderately small, once-

pinnate, the leaflets 4–8 pairs; petiole usually less than 1 cm. long, terete, tomentose like the young branchlets, often appearing to bear a gland because of abortion of lowermost pair of leaflets; rachis up to 10 cm. long, similar to the petiole, bearing sessile, concave glands at insertion of leaflet pairs; leaflets somewhat variable but mostly oblong, 2–6 cm. long and 1–2.5 cm. wide, bluntly acute to rounded or subtruncate-retuse (malformation?) apically, obliquely rounded basally, subglabrous above, lightly pubescent below except heavily so on the costa; stipules linear, caducous. Inflorescence an axillary, pedunculate head; peduncle 3–(7?) cm. long, tomentose, bearing a linear-lanceolate bract (this often caducous) above the middle; head condensed; floral bracts linear, about 2 mm. long, pubescent and ciliate. Flowers sessile, whitish; calyx campanulate-funnelform, about 1 mm. long, rufous-pubescent except at extreme base; corolla tubular or nearly so, about 7 mm. long, glabrous except on the lobes; ovary sessile, glabrous. Legume not known, but presumably similar to that of *P. rufescens*.

Panama and Colombia.

CHIRIQUÍ: Boquete, *Davidson 628*. COCLÉ: Penonomé, *Williams 49*.

The description is chiefly from the Chiriquí specimen (in immature flower). As far as can be determined from keys and rather incomplete descriptions, this specimen is *P. tubuliferum*, although no authentic specimens are available for comparison. It is similar to *P. rufescens* but differs in having more and generally smaller leaflets, and has the floral bracts less pronounced.

4. PITHECOLOBIUM VALERIOI (Britt. & Rose) Standl. in Field Mus. Publ. Bot. 18:509. 1937.

Cojoba Valerioi Britt. & Rose, in N. Am. Fl. 23:32. 1928.
Cojoba Standleyi Britt. & Rose, loc. cit. 1928.
Pithecolobium Standleyi Standl. loc. cit. 1937.

Shrub or small tree, the branchlets rufous-puberulent when young becoming glabrate, lenticellate. Leaves large, bipinnate, the pinnae 1 pair, the leaflets 2–5 (usually 3) pairs per pinna; petiole quite short, less than 1 cm. long, terete, puberulent, bearing an apicule about 4 mm. long terminally between insertion of the pinnae; pinnular rachis almost 10 cm. long, rufous-tomentulose, terete, bearing sessile, subcupular glands at insertion of leaflet pairs; leaflets ovate to elliptic, the terminal pair as much as 15 cm. long and 6 cm. wide, acute to short-acuminate apically, very obliquely blunt or rounded basally (the basal pair as small as 2.5 cm. long and 1 cm. wide, scarcely oblique basally, not strictly opposite), subglabrous above and below except on the costa, the veins prominent below; stipules linear, scarcely 2 mm. long. Inflorescence a pedunculate head arising slightly above the axil; peduncle 2–(6?) cm. long, puberulent, bearing a squamiform bract above the middle; head condensed, about 4 cm. in diameter; floral bracts linear-lanceolate, 2–3 mm. long, rufous-pubescent and ciliate. Flowers sessile, white; calyx cylindric, 2–3 mm. long, glabrous except tomentulose on the teeth; corolla tubular, about 12 mm. long, glabrous except tomentulose on the lobes; stamens about 18 mm.

Fig. 87. *Pithecolobium catenatum*

long, the staminal-tube included; ovary sessile, subglabrous. Legume apparently moniliform, about 10 cm. long, red, the seeds black, the valves twisting after dehiscence.

Costa Rica and Panama.

BOCAS DEL TORO: Chiriquí Lagoon, *H. von Wedel 2246, 2254;* Water Valley, *H. von Wedel 1723.*

The Water Valley specimen is rather poor, and had originally been determined as *Inga*. The species is poorly known, but seemingly is quite variable. The cited specimens are probably better regarded as conspecific with *P. Valerioi* and *P. Standleyi* than as distinct and coordinate with these species, although certain differences exist between collections of *P. Valerioi*, *P. Standleyi* and the cited specimens.

5. Pithecolobium catenatum Donn. Smith, in Bot. Gaz. 48:294. 1909.

Cojoba catenata Britt. & Rose, in N. Am. Fl. 23:32. 1928.

Tree, the branchlets ferruginous-tomentulose when young, longitudinally striate or rugose when dry, prominently lenticellate. Leaves large, twice-pinnate, the pinnae 1 pair, the leaflets 4–6 pairs per pinna; petiole 2–6 cm. long, terete, ferruginous-pubescent, subsulcate above, usually bearing a small, sessile gland apically; pinnular rachis 10–20 cm. long, similar to the petiole, bearing a small, crateriform gland at insertion of the pairs of leaflets; leaflets elliptic or obovate, the terminal pair quite large, 10–20 cm. long and 5–7.5 cm. wide, the basal pair 3–8 cm. long and 1.5–4.5 cm. wide, acute apically, inequilaterally acute or obtuse basally, subglabrous above except on the costa, lightly pubescent below or subglabrous except on the veins; stipules caducous. Inflorescence of very long pedunculate heads lateral from the axils of the older wood; peduncle 8–24 cm. long, usually with a squamiform bract above the middle, tomentulose; head condensed, about 4 cm. in diameter. Flowers sessile, white; calyx tubular, 2.5–4.5 mm. long, glabrous except puberulent on the teeth; corolla tubular, about 16 mm. long and 1.0–1.5 mm. wide, glabrous, longitudinally substriate, the lobes thick and brown-pubescent apically; stamens about 25 mm. long, the staminal tube included; ovary terete, lightly pubescent, 12- to 14-ovulate; style glabrous. Legume moniliform, terete, up to 18 cm. long, red, tomentose, short-stipitate, the valves twisting after dehiscence.

Costa Rica and Panama.

Bocas del Toro: Bastimentos, *H. von Wedel 2909;* Careening Cay, *H. von Wedel 2815;* Isla Colón, *H. von Wedel 576;* Old Bank Island, *H. von Wedel 1977, 2066;* without locality, *H. von Wedel 199.*

This species is especially marked by the unusually long peduncles.

6. Pithecolobium latifolium (L.) Benth. in Hook. Lond. Jour. Bot. 3:214. 1844.

Mimosa latifolia L. Syst. ed. 10, 1310. 1759.
Zygia arborescens St. Hil. Expos. Fam. Nat. 2:246. 1805, fide Britt. & Rose.
Inga latifolia Willd. Sp. Pl. 4:1020. 1806.
Calliandra latifolia Griseb. Fl. Brit. W. Ind. 225. 1860.
Feuilléea latifolia Ktze. Rev. Gen. Pl. 1:188. 1891.
Zygia latifolia Fawc. & Rendle, Fl. Jam. 4^2:150. 1920.
Pithecolobium chagrense Pittier, in Contr. U. S. Nat. Herb. 20:465. 1922.

Shrub or small tree, the branchlets glabrous, inconspicuously lenticellate. Leaves moderately large, bipinnate, the pinnae one pair, the leaflets 3–5 per pinna;

petiole very short, mostly 2–3 mm. long, callous, rugose, bearing a patelliform or subpeltate gland apically; rachis of pinna up to 10 cm. long, sulcate above, puberulent or subglabrous, bearing a small gland apically at insertion of terminal leaflets; leaflets elliptic, 5–15 cm. long and 1.5–6 cm. wide, the terminal pair opposite on the pinna, the penultimate pair alternate or lacking, the basal leaflet solitary on the outer side (sometimes basal leaf caducous), acute and short-acuminate apically, cuneate or subcuneate basally, slightly asymmetrical, glabrous above and below, with usually 3 prominent, ascending, arcuate lateral veins; stipules ovate. Inflorescence of fasciculate sessile heads (or very condensed spikes) lateral on the older branchlets, the axis scarcely 5 mm. long, pubescent; bracts ovate, about 1 mm. long. Flowers sessile, pinkish; calyx cupular, about 1 mm. long, pubescent apically on the minute teeth; corolla tubular, about 7 mm. long, only slightly expanded above, subglabrous except puberulent on the lobes, striate; stamens usually about 17 mm. long, the staminal tube slightly exserted; ovary subsessile, lightly pubescent; style exceeding the stamens, the stigma capitellate. Legume linear, about 12 cm. long and 2 cm. wide (immature?), flat, minutely puberulent, arcuate.

West Indies; Honduras to Panama; Colombia to Brazil and Bolivia.

BOCAS DEL TORO: Garay Creek, *H. von Wedel 2633;* Old Bank Island, *H. von Wedel 2014;* Water Valley, *H. von Wedel 868.* CANAL ZONE: "Chagres," *Fendler 90;* France Field, *Standley 30368;* Gatún, *Hayes 459; Pittier 2808.*

As with *P. longifolium, P. latifolium* appears to be a fairly constant species. It is quite similar to *P. glomeratum* and *P. cauliflorum,* two South American species doubtfully distinct from each other. *P. latifolium* is distinguished from *P. longifolium* in having a much shorter inflorescence, wider and often more numerous (5 vs. 3) leaflets.

7. PITHECOLOBIUM LONGIFOLIUM (H. & B.) Standl. in Field. Mus. Publ. Bot. 4:212. 1929.

Inga longifolia Humb. & Bonpl. ex Willd. Sp. Pl. 4:1010. 1806.
Mimosa ligustrina Vahl, Eclog. 3:34, *t. 27.* 1807, not Jacq. 1801, fide Benth
Inga Vahlianum DC. Prodr. 2:438. 1825.
Inga falciformis DC. loc. cit. 1825, fide Benth.
Pithecolobium ligustrinum Benth. in Hook. Lond. Jour. Bot. 3:213. 1844.
Pithecolobium glomeratum var. *spicatum* Seem. Bot. Voy. Herald, 116. 1852–53, fide Britt. & Rose.
Pithecolobium Vahlianum Benth. in Trans. Linn. Soc. 30:594. 1875.
Feuilléea longifolia Ktze. Rev. Gen. Pl. 1:185. 1891.
Zygia longifolia Britt. & Rose, in N. Am. Fl. 23:40. 1928.

Moderate-sized tree, the branchlets glabrous or nearly so, lenticellate but not prominently so. Leaves moderate, bipinnate, the pinnae 1 pair, the leaflets 3 to the pinna (terminal pair and outer member of reduced basal pair?); petiole short and condensed, 3–10 mm. long, rugose, callous basally, bearing between insertion of the pinnae a sessile patelliform or subpeltate gland; rachis of pinna usually about 2 cm. long, sulcate and puberulent above, commonly but not always bearing a gland between insertion of terminal pair of leaflets; leaflets narrowly ovate-lanceo-

Fig. 88. *Pithecolobium longifolium*

late, lanceolate or elliptic, 4–12 cm. long and 1.5–3.5 cm. wide, cuneate or subcuneate basally, usually bluntly acute or acuminate apically, glabrous on both sides, inconspicuously reticulate; stipules lanceolate, about 2 mm. long. Inflorescence lateral on older wood, of short, lax, fasciculate spikes; spikes about 2 cm. long, scarcely pedunculate, subglabrous; bracts lanceolate, about 1 mm. long, subpersistent. Flowers small, sessile, whitish or pinkish, fragrant; calyx cupular, about 1 mm. long, glabrous except the minute teeth puberulent or ciliate; corolla tubular-funnelform, 6–7 mm. long, glabrous; stamens many, about 16 mm. long, the staminal tube well exserted; ovary pubescent. Legume linear-arcuate, up to 30 cm. long and about 13 mm. wide, glabrous, flat and thin, short-stipitate, the seeds longitudinal.

Honduras to Panama; northern South America.

BOCAS DEL TORO: Water Valley, *H. von Wedel 653; Cooper & Slater 54b.* CANAL ZONE: R. Chagres, *Steyermark & Allen 16787;* R. Indio Hydrographic Station, *Steyermark 17418;* Tumba Vieja, *Steyermark & Allen 16745.* COCLÉ: Bismarck, *Williams 245;* El Valle, *Allen 108, 2765.* COLÓN: Santa Isabel, *Pittier 462.* DARIÉN: Boca de Cupé, *Allen 871.* PANAMÁ: R. Las Lajas, *Allen 1613;* R. La Maestra, *Allen 23.*

The species in Panama seems to exhibit stability unexpected in the genus. Similar to *P. latifolium* and other species, the differences, although minor, appear surprisingly constant.

Fig. 89. *Pithecolobium hymeneaefolium*

8. PITHECOLOBIUM HYMENEAEFOLIUM (H. & B.) Benth. in Hook. Lond. Jour. Bot. 3:198. 1844.

Inga hymenaeaefolia Humb. & Bonpl. ex Willd. Sp. Pl. 4:1008. 1806.
Mimosa hymeneaefolia Poir. in Lam. Encycl. Meth. Suppl. 1:38. 1810.
Pithecolobium panamense Walp. & Duchass. in Linnaea 23:746. 1850.

Shrub or small tree to a few meters tall; branchlets subglabrous, minutely lenticellate, with a few longitudinal lines or thin ridges and usually paired nodal thorns. Leaves moderate, bipinnate, the pinna bifoliolate; petiole mostly 2–4 cm. long, canaliculate above, glabrous, bearing apically a sessile, cupular gland; axis of the pinna up to 2 cm. long, like the petiole; mature leaflets asymmetrically ovate

or ovate-lanceolate, 6–13 cm. long and 2–5 cm. wide, bluntly acute apically, obliquely rounded basally, glabrous above and below except often barbate basally below on the narrow side; stipules modified as small to prominent recurved thorns or spines to either side of the petiolar insertion. Inflorescence of elongate, axillary, subterminal and terminal pedunculate spikes; peduncle 1.5–6 cm. long, subglabrous; floriferous portion of the spike mostly 3–6 cm. long, the axis tomentulose and few-sulcate, the flowers condensed; bractlets minute, ovate-subulate. Flowers large, sessile, whitish; calyx cupular, about 2 mm. long, tomentulose, the teeth short and somewhat irregular; corolla funnelform, usually about 1 cm. long, tomentulose without, valvate; stamens 5–6 cm. long, united basally into a prominently exserted staminal tube 2–4 cm. long; ovary sessile, pubescent; style (plus ovary) about 6 cm. long, the stigma capitellate. Legume 7–10 cm. long and about 15 mm. wide, falcate, compressed, tomentose, rugose, few-seeded, the seeds black.

Panama, Colombia, Venezuela.

CANAL ZONE: "north end of island" (Miraflores?), *P. White 124*; R. Chagres, *Steyermark & Allen 16790*; Salamanca Hydrographic Station, *Woodson, Allen & Seibert 1567*. PANAMÁ: Taboga Island, *Woodson, Allen & Seibert 1539*; Chepo, *Dodge, Hunter, Steyermark & Allen 16663*.

The corolla of the cited specimens is slightly shorter than dimensions given for the species by most authors. There is some uncertainty as to application of the Willdenow name and its interpretation by later authors.

9. PITHECOLOBIUM LANCEOLATUM (H. & B.) Benth. in Hook. Lond. Jour. Bot. 5:105. 1846.

Mimosa ligustrina Jacq. Fragm. Bot. 29, *pl. 32, f. 5*. 1801.
Inga lanceolata Humb. & Bonpl. ex Willd. Sp. Pl. 4:1005. 1806.
Mimosa lanceolata Poir. in Lam. Encycl. Meth. Suppl. 1:37. 1810.
Pithecolobium macrostachyum Benth. in Hook. Lond. Jour. Bot. 3:198. 1844, excl. syn. Vahl., fide Benth.
Pithecolobium ligustrinum Kltz. ex Benth. in Trans. Linn. Soc. 30:571. 1875, not Benth. 1844.
Pithecolobium macrosiphon Standl. in Contr. U. S. Nat. Herb. 20:191. 1919, fide Standl. & Steyerm.
Pithecolobium Winzerlingii Britt. & Rose, in N. Am. Fl. 23:193. 1928, fide Standl. & Steyerm.

This species, to the best of my knowledge, has not yet been collected in Panama, but is known from Mexico, northern Central America and Costa Rica, and northern South America. It thus can be expected in Panama also. It is a small, armed tree similar vegetatively to *P. oblongum* except that the leaflets average larger. The floriferous portion of the spike is considerably more elongate (4–12 cm. long) than in *P. oblongum*, and the corolla is 5–6 mm. long. The ovary is subsessile, the legume similar to *P. oblongum* although perhaps somewhat larger. As with *P. dulce*, the aril of the seeds is said to be edible and used for making a beverage suggestive of lemonade. *P. lanceolatum* can scarcely be distinguished from *P. pachypus* Pittier except in fruit. *P. pachypus*, a species of Salvador,

Guatemala, and Mexico, has a significantly broader, stockier fruit than does *P. lanceolatum*, but insufficient fruiting material is on hand to appraise accurately the delimitation and distribution of these species.

10. PITHECOLOBIUM OBLONGUM Benth. in Hook. Lond. Jour. Bot. 3:198. 1844.

Feuilléea oblonga Ktze. Rev. Gen. Pl. 1:188. 1891.
Pithecolobium paniculatum Pittier, in Contr. U. S. Nat. Herb. 20:462. 1922.
Pithecolobium pulchellum Pittier, loc. cit. 1922.
Pithecolobium microstachyum Standl. in Jour. Wash. Acad. 13:439. 1923.
Pithecolobium Pittieri Britt. & Killip, in Ann. N. Y. Acad. Sci. 35:125. 1936.

Fig. 90. *Pithecolobium oblongum*

Small or bushy tree to several meters; branchlets essentially glabrous, with a few longitudinal lines or thin ridges and many prominent lenticels. Leaves moderately small, bipinnate, each pinna bifoliolate; petioles mostly 1–3 cm. long, slender, subglabrous, somewhat flattened, canaliculate above, bearing a short-columnar, concave gland apically above; axis of the pinna mostly 1 cm. or less long, similar to the petiole except the apical gland sometimes obsolete; leaflets asymmetrically ovate, oblong or obovate, up to almost 6 cm. long and 3.5 cm. wide, obtuse to rounded or subtruncate apically, obliquely obtuse basally, glabrous above and below except barbate basally on the narrow side below; stipules modified as small or moderate thorns or spines to either side of the petiole, a few mm. to 1 cm. long or longer. Inflorescence an axillary panicle, usually subterminal, consisting of a

number of pedunculate spikes; peduncles slender, usually 1–2 cm. long at maturity, lightly pubescent or subglabrous; floriferous portion of spike 5–20 mm. long, condensed apically and somewhat more lax baseward; bractlets ovate-lanceolate, scarcely 1 mm. long, persistent, pilosulous. Flowers small, sessile, whitish; calyx cupular, little over 1 mm. long, shallowly lobed, puberulent, 5-angled; corolla funnelform, 3–4 mm. long, valvate, puberulent at least apically; stamens about 8–9 mm. long, united below into a short staminal tube; ovary stipitate, glabrous, the stipe almost 1 mm. long. Legume linear-circinate, up to 10 cm. long and about 1 cm. wide, frequently coiled upon itself, dehiscent, compressed but turgid at and indented between the seeds, nearly glabrous, reddish; seeds ovoid, lustrous-black.

Mexico to Panama.

CANAL ZONE: Farfan Beach, *Hunter & Allen 446*; without locality, *Allen 1632*; *Hayes 313, 761*; *Seemann 403*. PANAMÁ: beach, Panama Vieja, *Allen 827*; *Bro. Paul 788*; beach, San Carlos, *Allen 1133*; Bella Vista, *Killip 12019*; Punta Paitilla, *Piper 5120*.

No authentic specimens of *P. oblongum* have been available for comparison with the cited Panamanian material. Bentham's description fits the cited specimens as far as it goes, but it is scarcely complete and comprehensive in a modern sense. Yet, it seems very likely that our specimens are *P. oblongum*, a species described from a Panamanian type, especially in that they key to or close to *P. oblongum* as interpreted by various authors. Specimens of *P. microstachyum* Standl. seem to differ from our material only within the allowable limits of specific variation. *P. pulchellum* Pittier and *P. Pitteri* Britt. & Killip differ from the Panamanian material inconstantly and in a very minor fashion. There is also apparent intergradation to *P. unguis-cati*, restricted (for convenience?) to the West Indies. The species is evidently a sea beach plant.

11. PITHECOLOBIUM DULCE (Roxb.) Benth. in Hook. Lond. Jour. Bot. 3:199. 1844.

Mimosa dulcis Roxb. Pl. Coromand. 1:67. 1795.
Inga dulcis Willd. Sp. Pl. 4:1005. 1806.
Inga pungens H. & B. ex Willd. loc. cit. 1004. 1806, fide Benth.
Mimosa pungens Poir. in Lam. Encycl. Meth. Suppl. 1:36. 1810.
Inga javana DC. Prodr. 2:436. 1825, fide Benth.
Mimosa unguis-cati Blanco, Fl. Filip. 731. 1837, non L., fide Benth.
Acacia obliquifolia Mart. & Gal. in Bull. Acad. Brux. 10^2:317. 1843, fide Benth.
Inga leucantha Presl, Bot. Bem. 65. 1844, fide Benth.
Feuilléea dulcis Ktze. Rev. Gen. Pl. 1:184. 1891.
Pithecolobium littorale Britt. & Rose ex Record, in Trop. Woods 11:15. 1927, fide Standl. & Steyerm.

Small to medium tree, often flowering when small and shrub-like, the branchlets puberulent or subglabrous becoming glabrous in age. Leaves small, bipinnate, each pinna bifioliolate; petiole mostly 1–2 cm. long, subglabrous or lightly puberulent, margined and sulcate above especially apically, callous basally, bearing a concave gland at insertion of the pinnae; axis of the pinna like the petiole, up to 1 cm. long, the gland frequently smaller than the petiolar gland; leaflets 2 per pinna, mostly inequilaterally oblong, 2–6 cm. long and 1–3 cm. wide, obliquely obtuse or

rounded basally, blunt or rounded apically, glabrous except barbate basally below; stipules modified as scarcely noticeable to moderate spines or thorns on either side of the petiole. Inflorescence a terminal or subterminal panicle of pedunculate heads; peduncles about 1 cm. long or longer at anthesis, puberulent; head globose, about 15 mm. in diameter, several-flowered, compact; bracts scarcely 1 mm. long. Flowers small, whitish; calyx cupular, about 1 mm. long, canescent-tomentulose; corolla funnelform, 2–3 mm. long, tomentulose, the lobes about 1 mm. long; stamens many, about 8 mm. long, united below into a staminal tube for about half their length, glabrous; ovary pubescent, stipitate. Legume torulose or subtorulose, up to 12 cm. long and 8–15 mm. wide, coiled, glabrous or puberulent, dehiscent, the valves twisting after dehiscence.

Mexico to northern South America.

CANAL ZONE: Balboa, *Standley 30842*.

This species is very similar to *P. unguis-cati*, a species "not known to occur in Panama," from which it differs in having pubescent rather than glabrous flowers.

12. PITHECOLOBIUM MANGENSE (Jacq.) Macbr. in Contr. Gray Herb. 59:3. 1919.

Mimosa mangensis Jacq. Enum. Pl. Carib. 34. 1760.
Mimosa parvifolia Sw. Fl. Ind. Occ. 984. 1800.
Acacia parvifolia Willd. Sp. Pl. 4:1086. 1806.
Mimosa antillarum Lam. ex Poir. in Lam. Encycl. Meth. Suppl. 1:80. 1810.
Acacia micrantha Desv. ex Ham. Prodr. Fl. Ind. Occ. 60. 1825, fide Benth.
Inga marthae Spreng. ex DC. Prodr. 2:441. 1825, fide Benth.
Pithecolobium parvifolium Benth. in Hook. Lond. Jour. Bot. 3:223. 1844.
Feuilléea mangensis Ktze. Rev. Gen. Pl. 1:186. 1891.
Enterolobium mangense Fawc. & Rendle, Fl. Jam. 4^2:151. 1920.
Chloroleucon mangense Britt. & Rose, in N. Am. Fl. 23:38. 1928.
Cathormium mangensis Dugand, in Apunt. Hist. Nat. Dept. Atl. 32. 1933, fide Britt. & Killip.

Shrub or small tree, armed at most (older) nodes with paired spines, the branchlets glabrate and moderately lenticellate, frequently flexuous in active growth, bearing large, ovoid, axillary buds with prominent bud-scales. Leaves small, twice-pinnate, the pinnae 4–10 pairs, the leaflets 8–30 pairs; petiole slender, usually 1–2 cm. long, more or less puberulous, flattened on the upper side and bearing a small clavate gland, usually below the middle; primary rachis similar, sulcate above, usually bearing a sessile, concave gland between some or at least the terminal pair of pinnae; rachis of pinna mostly 2–4 cm. long, pubescent, more or less terete; leaflets small, linear, usually about 6 mm. long and little over 1 mm. wide, somewhat falcate, asymmetrically acute apically, obliquely rounded or truncate basally, lightly pubescent or subglabrous, the veins few and prominent below; stipules at most nodes becoming modified as spines, those straight or slightly curved, as much as 15 mm. long. Inflorescence an axillary, pedunculate head; peduncle slender, about 2 cm. long, somewhat puberulent; bracts linear, minute, caducous. Flowers white, sessile; calyx cupuliform-campanulate, about 2 mm. long, glabrous except

perhaps on the lobes; corolla tubular-funnelform, 4–8 mm. long, glabrous except the lobes puberulent-tipped; stamens 12 or more mm. long, the staminal tube about equalling the corolla. Legume linear, 6–14 cm. long and 10–12 mm. wide, compressed or nearly flat but thick, fleshy-coriaceous, glabrous, reticulate-veined, curved or nearly straight.

Panama and northern South America; Jamaica.

VERAGUAS: Santiago, *Allen 1082*.

This species is poorly represented in the herbarium, its variability and exact taxonomic position uncertain.

13. PITHECOLOBIUM PSEUDO-TAMARINDUS (Britt.) Standl. in Field Mus. Publ. Bot. 4:212. 1929.

Jupunba pseudo-Tamarindus Britt., in N. Am. Fl. 23:193. 1928.

Unarmed, buttressed tree up to 18 m. tall, the branchlets angulate and ferruginous-tomentulose. Leaves twice-pinnate, the pinnae mostly 12–16 pairs, each pinna with about 30–40 pairs of leaflets; petiole 1–4 cm. long, terete, bearing 1–3 sessile glands towards or above the middle; rachis up to 20 cm. long, tomentulose, bearing sessile glands between all pairs of pinnae; pinnae mostly opposite, 6–9 cm. long, the rachis tomentulose, gland-bearing between the upper leaflets; leaflets narrowly oblong, 5–7 mm. long and almost 2 mm. wide, apically obtuse or rounded, basally sessile and obliquely rounded, glabrous, lighter below, the costa central, the secondary nerves only moderately prominent. Inflorescence subumbellate, axillary, the peduncle 2–12 cm. long, ebracteate, the pedicels 4–6 mm. long. Flowers (type specimen in fruit) white, the center (terminal) one of the umbel somewhat larger (as in "*Samanea*"); calyx campanulate, about 2 mm. long, puberulent, the teeth 5, triangular, about 0.5 mm. long; corolla funnelform, about 7 mm. long, lightly pubescent without, the lobes 5, nearly as long as the tube; stamens many, about 25 mm. long, united only for the basal 3 mm., glabrous; anthers minute; ovary cylindric, about 3 mm. long, tomentulose, subtruncate apically, several- (about 14-) ovulate in 2 rows; style glabrous. Legume circinate, 10–12 mm. wide, lightly constricted and falsely septate between the 3–5 seeds, the valves thin, reddish-brown, sparsely strigillose or almost glabrous.

BOCAS DEL TORO: Bocas Island, *Cooper 461* (fruit); Chiriquí Lagoon, *H. von Wedel 1132* (flower).

The species is similar to some of the West Indian "Jupunbas" and "Abaremas." It had been known only from the type *(Cooper 461;* in fruit), but the von Wedel specimen (flowers only) appears to be the same species although the peduncle of the latter is markedly more elongate than in the type. The above description is pieced from both specimens.

14. PITHECOLOBIUM BARBOURIANUM Standl. in Contr. Arn. Arb. 5:74, *pl. 11*. 1933.

Unarmed tree, the branchlets fulvous hirsute-tomentose, slender. Leaves

moderately large, twice-pinnate, the pinnae 8–11 pairs, the leaflets mostly 9–16 pairs per pinna; petiole 1–2 cm. long, somewhat thick, densely tawny hirsute, bearing a sessile, irregular, shallowly crateriform gland near the apex; primary rachis 5–12 cm. long, subterete, pubescent like the petiole, bearing similar solitary glands below insertion of each pair of pinnae; pinnular rachis 3–6 cm. long, pilose, glandular at most upper nodes; leaflets oblong or oblong-trapezoidal, 5–10 mm. long and 3–6 mm. wide, apically obtuse or rounded, basally oblique, glabrous (except sometimes on the depressed costa) above, lighter and pilose below, especially on the costa, the secondary veins prominent, the margins subrevolute and adpressed-ciliate. Inflorescence of axillary, pedunculate heads; peduncles usually geminate, slender, 4–6 cm. long, pilose; head about 1 cm. in diameter, multiflorate, very condensed; floral bracts obovate-spatulate, about 2 mm. long. Flowers sessile, apparently inconspicuously dimorphic (terminal flower of head usually grosser, its ovary evidently not functional, the staminal column enlarged); calyx funnelform, about 3 mm. long, golden-brown hirsutulous, briefly and obtusely 5- to 6-dentate; corolla apparently funnelform, about 4 mm. long (mature bud), densely golden-hirsute without; stamens about 13, the filaments briefly united below, glabrous, the anthers small, eglandular; ovary pilose, subsessile. Legume not known.

CANAL ZONE: Barro Colorado Island, *Shattuck 237*.

The species is known only from the type collection. Without fruit or mature flower its affinities are difficult to establish. It would seem, however, to fall near the well-represented *P. Saman*.

15. PITHECOLOBIUM COSTARICENSE (Britt. & Rose) Standl. in Trop. Woods 34:40. 1933.

Cojoba costaricensis Britt. & Rose, in N. Am. Fl. 23:31. 1928.

Moderate-sized, spreading tree, the branchlets ferruginous-tomentose becoming more or less glabrate in age, lenticellate. Leaves moderately large, twice-pinnate, the pinnae 4–9 pairs, the leaflets mostly 10–14 pairs per pinna; petioles mostly 2–4 cm. long, terete, short-tomentose, eglandular or inconspicuously glandular, scarcely callous basally; primary rachis (petiolar extension) like the petiole, bearing small, erect, truncate or concave glands between insertion of pairs of pinnae; pinnular rachis similar, but the glands frequently obsolete between the leaflets; leaflets ovate-lanceolate, 10–25 mm. long and 5–10 mm. wide, bluntly acute apically, obliquely rounded or subtruncate basally, subglabrous except puberulent on the costa, dull and inconspicuously reticulate above, lighter and more obviously reticulate below. Inflorescence of solitary pedunculate heads from older axils, the peduncle 3–8 cm. long, tomentose, eglandular; head 3–4 cm. in diameter, the flowers crowded; bracts minute or caducous. Flowers white, sessile; calyx cupular-tubular, about 2 mm. long, subglabrous except rufous-tomentulose on the teeth; corolla tubular, approximately 1 cm. long, glabrous, the lobes scarcely expanded; stamens about 16 mm.

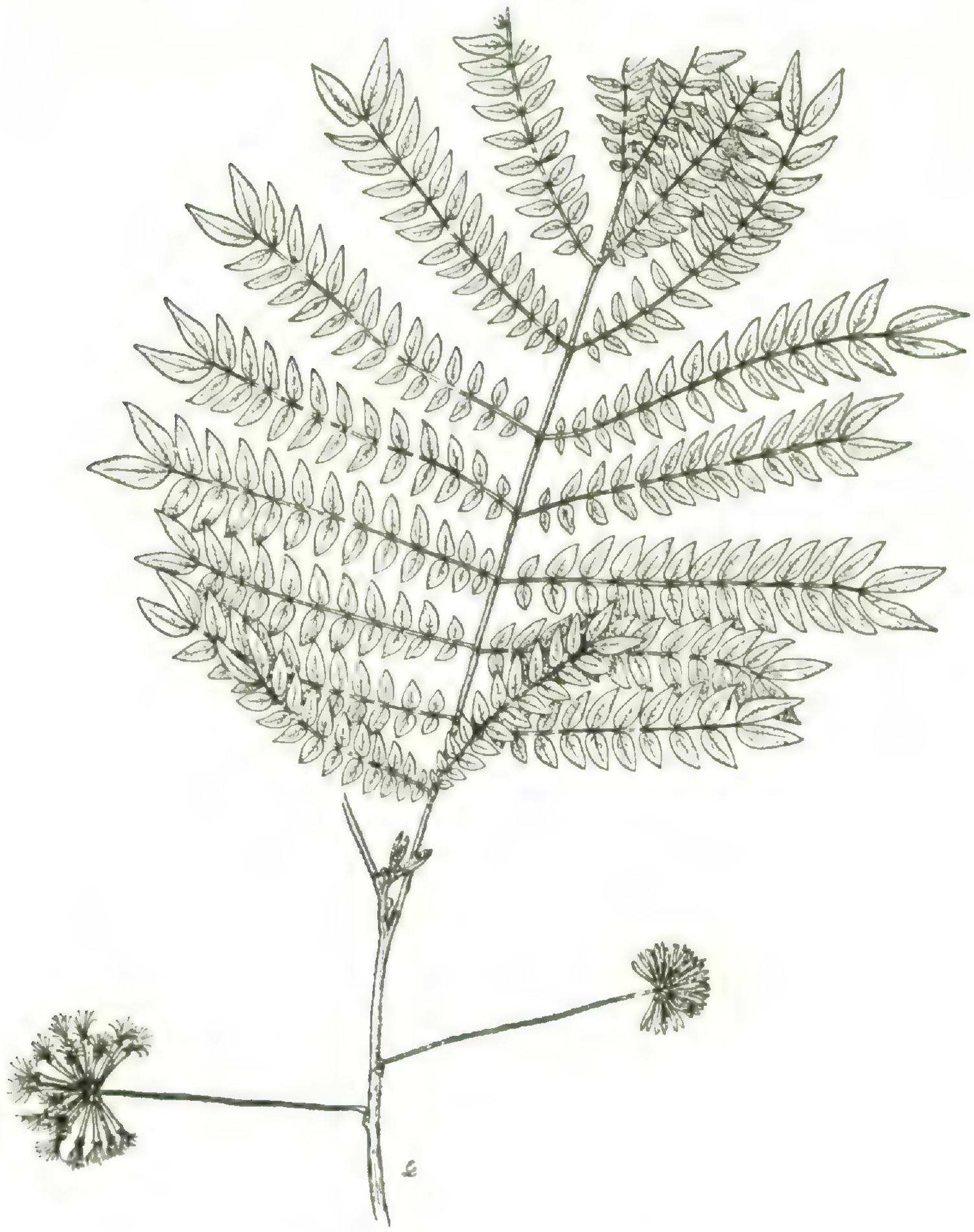

Fig. 91. *Pithecolobium costaricense*

long, glabrous, the staminal tube included; ovary subglabrous, very short-stipitate. Legume moniliform-subterete, reddish, the valves twisting after dehiscence.

Costa Rica and Panama.

CHIRIQUÍ: R. Chiriquí Viejo, *P. White 22*.

The *P. White 22* specimen is sterile, but seems on vegetative characters to be *P. costaricense*, a species to be expected in Panama. *P. chazutense* Standl., of Peru, and several Central American species are quite similar to *P. costaricense*.

16. PITHECOLOBIUM MACRADENIUM Pittier, in Contr. U. S. Nat. Herb. 20:465. 1922.

A moderate-sized tree, the branchlets more or less pubescent. Leaves moder-

ately large, twice-pinnate, the pinnae usually 3 pair, each bearing 5–8 pairs of leaflets; petioles 3.5–7 cm. long, minutely pubescent; primary rachis (petiolar extension) similar, bearing between insertion of the basal pair of pinnae a large, subcupular gland as much as 1 cm. long (possibly a disease condition), bearing between upper pairs of leaflets smaller glands or these more or less obsolete; rachis of pinna similar, bearing small glands between insertion of the pairs of leaflets; leaflets ovate or rhombic-ovate, 2–5 cm. long and 1–2.2 cm. broad, sessile, rounded apically, inequilateral basally, glabrous above except pubescent on the costa, paler and more or less pilosulous beneath; stipules linear, caducous. Inflorescence of axillary, pedunculate, condensed umbels or very short spikes; peduncles 5–6 cm. long, ferruginous-pubescent; flowers short-pedicellate, the pedicels 2.5 mm. long and sparsely puberulous. Flowers white, small; calyx campanulate, about 3.5 mm. long, puberulous, the teeth short, subacute; corolla funnelform, 6–6.5 mm. long, the tube glabrous, the lobes lanceolate, acute, and minutely brownish-pubescent; staminal tube included; pistil about 15 mm. long; ovary short-stipitate, glabrous. Legume about 10 cm. long and 2 cm. broad, thick, strongly arcuate, compressed, transversely sulcate between the seeds, short-stipitate.

Panama.

CANAL ZONE: Monte Lirio, *Christopherson 196*.

The species is known only from the type (U. S. Nat. Herb.). The above description is taken primarily from Pittier's original description. The most remarkable character of the species seems to be the very large gland between the basal pair of pinnae. I am familiar with no other species of the MIMOSOIDEAE bearing a gland of such proportions, and if this is a constant character not merely confined to an aberrant specimen, it may serve for ready identification of the species.

17. PITHECOLOBIUM SAMAN (Jacq.) Benth. in Hook. Lond. Jour. Bot. 3:216. 1844.

Mimosa Saman Jacq. Fragm. Bot. 15, *pl. 9*. 1800.
Inga cinerea H. & B. ex Willd. Sp. Pl. 4:1024. 1806, fide Benth.
Mimosa pubifera Poir. in Lam. Encycl. Meth. Suppl. 1:47. 1810.
Inga salutaris HBK. Nov. Gen. & Sp. 6:304. 1824, fide Benth.
Calliandra tubulosa Benth. in Hook. Lond. Jour. Bot. 3:101. 1844, fide Benth.
Pithecolobium cinereum Benth. loc. cit. 216. 1844.
?Acacia propinqua A. Rich. Ess. Fl. Cub. 466. 1845, fide Benth.
Calliandra Saman Griseb. Fl. Brit. W. Ind. 225. 1861.
Albizzia Saman F. Muell. Sel. Extra-Trop. Pl. 27. 1891, fide Rock, Legum. Pl. Hawaii.
Feuilléea Saman Ktze. Rev. Gen. Pl. 1:189. 1891.
Enterolobium Saman Prain ex King, in Jour. Asiat. Soc. Bengal 66^2:252. 1897.
Samanea Saman Merrill, in Jour. Wash. Acad. 6:46. 1916.

A large, spreading, unarmed tree, the branchlets aureo-pubescent becoming glabrate, sparingly lenticellate. Leaves large, twice-compound, the pinnae 2–6 pairs, each pinna with 2–8 pairs of leaflets (terminal pinnae usually with the more

Fig. 92. *Pithecolobium Saman*

numerous leaflets); petioles mostly 4–6 cm. long, canescent- or yellowish-tomentose, somewhat sulcate above; primary rachis (petiolar extension) 4–6 cm. long, similar to the petiole, bearing at or just below insertions of each pair of pinnae a small, sessile, subcupuliform, laterally extended gland; axis of the pinna like the primary rachis except the glands between (slightly below) insertions of the leaflet pairs smaller; leaflets asymmetrically ovate, oblong or obovate, up to about 4 cm. long and 2 cm. wide, obtuse or rounded apically, obliquely obtuse or rounded basally, puberulent or subglabrous and lustrous above, yellow-tomentulose below;

stipules caducous. Inflorescence of 1 to few pedunculate umbels axillary and subterminal on the branchlets; peduncles at anthesis 4–8 cm. long, tomentose, sulcate; umbels congested, the pedicels mostly 1–3 mm. long (except central flower sessile); bracts (except central flower) lanceolate, about 3 mm. long. Flowers whitish or pinkish, dimorphic; central (sessile) flower of umbel larger, persistent, its calyx campanulate, with 10 teeth, about 5 mm. long and 3–4 mm. wide, its staminal column gross and thick but the many stamens relatively short, its ovary ovulate but comparatively underdeveloped, this flower surrounded by 5 oblanceolate bracts about 5 mm. long; remaining (pedicellate) flowers first to fall, their calyx funnelform, about 5 mm. long and only 1–2 mm. wide, 5-toothed, aureo-tomentose; their corolla funnelform, about 1 cm. long, valvate, aureo-pubescent apically only; their stamens about 3.5 cm. long, the staminal-tube included; their ovaries sessile, subglabrous except pubescent at base of style, the style becoming more or less glabrous apically and about equalling the stamens. Legume linear or linear-oblong, reported as much as 20 cm. long and 2 cm. wide, straight or slightly curved, glabrate, the valves thick, the margins prominent, indented and septate between the seeds, the seeds transverse.

Mexico, Central America, South America: naturalized in West Indies and Old World tropics.

BOCAS DEL TORO: Almirante, *Cooper 442*. CANAL ZONE: several localities, sterile specimens. HERRERA: Divisa, *Allen 4433*. VERAGUAS: Santa Fe, *Allen 4437*.

A well-known and frequently abundant species in Central America, the leaves and pods of which are often relished by stock. The wood is of local importance and the pulp of the pods is said to be edible. The most common English name for this species is "rain tree."

SPECIES OF PITHECOLOBIUM OF DOUBTFUL OCCURRENCE IN PANAMA

PITHECOLOBIUM COGNATUM Benth.

Mamei railway station (*S. Hayes 166; Seemann s. n.*), fide Hemsl. Biol. Centr.-Am. Bot. 1:359. 1888.

The cited specimens, which I have not seen, are possibly *P. latifolium*. *P. cognatum* (as *Zygia cognata*), fide Britt. & Rose (N. Am. Fl. 23:39. 1928), is restricted to Mexico.

PITHECOLOBIUM FRAGRANS Benth.

Hacienda de San Juan, "Veraguas" *(Seemann 1190)*, fide Benth. in Trans. Linn. Soc. 30:592. 1875; and Hemsl. Biol. Centr.-Am. Bot. 1:360. 1888.

This species is regarded as a new genus, *Pseudalbizzia* by Britton & Rose (N. Am. Fl. 23:48. 1928), and is according to them restricted to the West Indies. It has been variously interpreted as *Acacia Berteriana, Inga fragrans, Pithecolobium Berteriana, Acacia Balbisii, Acacia littoralis, Albizzia Berteriana,* etc. Without seeing the Seemann specimen it is impossible to know to what entity Britton &

Rose refer this Panamanian specimen, since they restrict *Pseudalbizzia* to the West Indies. It is likely close to *Pithecolobium costaricense* if really a *Pithecolobium* (in the broad sense).

3. ENTEROLOBIUM Mart.

ENTEROLOBIUM Mart. in Flora 20:Beibl. 117. 1837.

Feuilléea Ktze. Rev. Gen. Pl. 1:182. 1891, in part.

Unarmed trees, usually large, the branchlets pubescent or glabrous. Leaves bipinnate, moderate or large, 2- or few-ranked; petiole prominent, bearing a gland usually near the middle; pinnae few to many, opposite, the rachis bearing glands especially terminally; leaflets usually numerous and small, inequilateral; stipules inconspicuous, caducous. Inflorescence of solitary to fasciculate pedunculate heads, axillary, or paniculate by insertion at defoliate nodes; peduncles slender; heads small, globular; flowers condensed, sessile, small; bracts small and inconspicuous. Flowers whitish; calyx campanulate to tubular-funnelform, valvate, briefly 5-dentate; corolla more or less funnelform, 5-lobed, valvate, about double the calyx; stamens 10 to many, exceeding the corolla, united below into a short, included staminal tube; anthers small, eglandular, quadrangular; ovary sessile, several-ovulate; style slender, equalling or exceeding the stamens, the stigma small. Legume diagnostic, circinnate or reniform, coiled into a complete or nearly complete circle, compressed or almost flattened but nevertheless somewhat fleshy, usually glabrous and lustrous, fairly broad, ligneous, indehiscent, septate between the seeds, the seeds transverse.

Mexico to Argentina. Introduced into Pacific Islands and elsewhere.

This small American genus (8 or less species, mostly South American) is retained separate from *Pithecolobium* (and *Albizzia*) following traditional practice. Nearly all students of the group have realized that *Enterolobium* probably constitutes no more than a section of *Pithecolobium* (in the broader sense), but for convenience have retained the genera separate. Morphologically the distinctiveness of *Enterolobium* rests mostly with the unusual, coiled legume.

a. Flower uniformly and densely ferruginous-tomentulose; petiole, rachis, and peduncle ferruginous-tomentulose; leaflets up to 60 or more pairs per pinna, only 2–4 mm. long ..... 1. E. SCHOMBURGKII
aa. Calyx and corolla canescent-tomentulose at tips of lobes; petiole, rachis, and peduncle usually subglabrous, not ferruginous; leaflets 15–30 pairs per pinna, 8–15 mm. long ..... 2. E. CYCLOCARPUM

1. ENTEROLOBIUM SCHOMBURGKII Benth. in Trans. Linn. Soc. 30:599. 1875.

Pithecolobium Schomburgkii Benth. in Hook. Lond. Jour. Bot. 3:219. 1844.

Feuilléea Schomburgkii Ktze. Rev. Gen. Pl. 1:189. 1891.

Slender, erect tree, the branchlets ferruginous-tomentulose or puberulent. Leaves moderate, twice-compound, 2-ranked, the leaflets very small; petioles mostly 2–3 cm. long, terete, ferruginous-tomentulose, bearing an ovoid, sessile gland on the upper surface more or less at the middle; rachis usually 6–20 cm. long, fer-

Fig. 93. *Enterolobium Schomburgkii*

ruginous-tomentulose, ridged above along the center, bearing a small prominence or gland between or just below insertion of all or most pairs of pinnae; pinnae generally about 20 pairs, opposite or subopposite, the pinnular rachis mostly 4–7 cm. long, bearing glands (hidden by leaflets) between insertion of the terminal 1 to few pairs of leaflets; leaflets many (about 60?) pairs per pinna, linear or linear-oblong, more or less falcate, only 2–4 mm. long, obliquely rounded basally, inequilaterally obtuse or acute apically, the costa excentric, glabrous above, pubescent below; stipules early caducous. Inflorescence of 1 to few pedunculate heads from several foliate or defoliate nodes of the terminal branchlets; peduncles about 2 cm. long, ferruginous-tomentulose; heads globular, about 1 cm. in diameter (in bud), many-flowered; bracts minute. Flowers small, sessile, whitish; calyx funnelform, about 2 mm. long, ferruginous-tomentulose without, valvate; corolla tubular-funnelform, about 4 mm. long, ferruginous-tomentulose without, valvate; stamens 10 (or more?), about 1 cm. long, the filaments united below for less than half their length into a short, included staminal tube; ovary pubescent, terete.

Legume completely coiled upon itself into a circle about 5–7 cm. in diameter, compressed or almost flattened, 2–3 cm. wide, glabrous.

Mexico and Guatemala to Brazil.

CHIRIQUÍ: San Felix, *Pittier 5273*. PANAMÁ: Cerro Jefe, *Allen 3434;* Rio Indio drainage, *Barbour 1058*.

By reason of the distinctive fruit, this species is graced with many local, often picturesque, common names (viz. Brazil—*orelha de macaco,* "monkey's ear"; *orelha de preto,* "nigger's ear"; etc., etc.). This species seems to have little commercial use in South America, although it is reported of value for lumber and ties in northern Central America. Except when in fruit this and the following species might be mistaken for *Albizzia caribaea* and *A. malacocarpa* or *A. idiopoda*.

2. ENTEROLOBIUM CYCLOCARPUM (Jacq.) Griseb. Fl. Brit. W. Ind. 226. 1861.

Mimosa cyclocarpa Jacq. Fragm. Bot. 30, *t. 34, f. 1*. 1801.
Inga cyclocarpa Willd. Sp. Pl. 4:1026. 1806.
?Prosopis dubia HBK. Nov. Gen. & Sp. 6:309. 1824, fide Benth.
Pithecolobium cyclocarpum Mart. in Flora 20[2]:Beibl. 115. 1837.
Mimosa Parota Sessé & Moç. Pl. Nov. Hisp. 257. 1887.
Feuilléea cyclocarpa Ktze. Rev. Gen. Pl. 1:184. 1891.

Spreading tree, often very large and buttressed on the trunk, the branchlets puberulent to glabrous, smooth. Leaves moderate, twice compound, few-ranked; petiole up to about 8 cm. long, subterete, swollen basally, glabrous or somewhat puberulent, bearing an ovoid gland on the upper side usually near the middle; rachis up to 15 or more cm. long, shallowly sulcate and submarginate above, glabrous or somewhat puberulent, bearing subcupular glands between the terminal and usually penultimate insertions of the pinnae; pinnae 4–15 pairs, opposite on the rachis, the pinnular rachis with sessile or partly sunken, oblong, concave glands near insertion of the terminal 1–4 pairs of leaflets; leaflets 15–30 pairs, opposite, small, inequilaterally oblong or oblong-subfalcate, 8–15 mm. long, obliquely rounded basally, obliquely acute-mucronate apically, subglabrous and dark above, appressed-puberulent and lighter below, the costa excentric; stipules not evident. Inflorescence of 1–3 pedunculate heads from several foliate or (more frequently) defoliate nodes of the young branchlets; peduncle 2–4 cm. long, puberulent or subglabrous; head globular, 10–15 mm. in diameter, multiflorate; bracts minute. Flowers small, sessile, whitish; calyx short tubular-campanulate, about 3 mm. long, puberulent or subglabrous on the tube, canescent-tomentulose on tips of the lobes, valvate in bud; corolla tubular-funnelform, 5–6 mm. long, subglabrous except canescent-tomentulose toward the tip, valvate in bud; stamens many, up to 12 mm. long, filaments united into a staminal tube for about half their length; anthers quadrangular, unappendaged; ovary glabrous, subsulcate laterally; style about equalling or slightly exceeding the stamens. Legume reniform, about 10 cm. across and 3–6 cm. wide, compressed, glabrous, lustrous, curved into a nearly complete circle.

Mexico to northern South America.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 94.* CANAL ZONE: Balboa, *Standley 3084* (sterile). CHIRIQUÍ: Progreso, *Cooper & Slater 283* (sterile). COCLÉ: La Venta, *Muenscher 16326;* Penonomé, *Williams 288.* PANAMÁ: Chepo, *Kluge 35;* Punta Paitilla, *Piper 5139.*

The species apparently grades into *E. timbouva* Mart. of eastern and southern South America. *E. cyclocarpum* is said to have a number of local uses, such as the pulp of the fruit for food and as a soap substitute, a gum from the trunk as a remedy, and the wood of the harder specimens, easily worked and polished and seasoning well, as a decorative or cabinet wood. Except in fruit the species may easily be confused with *Albizzia malacocarpa* and *A. idiopoda* (northern Central America): the leaflets in these species of *Albizzia,* however, are not as markedly mucronate apically as with *E. cyclocarpum.*

4. ALBIZZIA Durazzini

ALBIZZIA Durazz. Mag. Tosc. 3:11. 1772.

Sericandra Raf. Sylva Tellur. 119. 1838.
Serianthes Benth. in Hook. Lond. Jour. Bot. 3:84. 1844.
Besenna A. Rich. Tent. Fl. Abyss. 1:253. 1847.

Trees or shrubs, mostly unarmed, pubescent or glabrous. Leaves few-ranked, usually large, bipinnate, the pinnae and leaflets few to many pairs; petiole glandular, the gland usually borne near or below the middle, less frequently above the middle, but always below insertion of the lowermost pair of pinnae; petiolar gland concave, longitudinally oblong and sunken in the petiole to orbicular and erect; rachis and pinnular rachis usually also bearing glands, especially towards the tips; leaflets small and linear to moderate and ovate, variously pubescent; stipules usually caducous or lacking. Inflorescence of usually subterminal, axillary, pedunculate heads, spikes, or umbels. Flowers pentamerous, synsepalous and sympetalous, regular, almost invariably perfect, white to pink; calyx campanulate to tubular, toothed apically, usually pubescent; corolla mostly funnelform, valvate; stamens numerous, united below into a staminal tube which is usually included; anthers small, eglandular. Legume linear to oblong, relatively broad but very flat and thin, straight, dry, not septate, indehiscent or tardily dehiscent, the valves never contorted nor elastically dehiscent, the seeds transverse.

Pantropical but relatively rare in the New World.

Albizzia is primarily an Old World genus, scarcely distinguishable from *Enterolobium* and *Pithecolobium* (primarily New World). The traditional means of distinguishing the genus (on basis of the legume) is highly inconvenient. New supplementary characters are thus utilized here (especially position of glands: whether on petiole or rachis only) which seem definitely more practical in separating *Albizzia* from *Pithecolobium.* Separation of *Albizzia* from *Enterolobium* is more difficult in the absence of fruit, but since few species are then involved individual specific characters usually serve to make determination possible. Certain

species of *Acacia* so resemble a few species of *Albizzia* that detailed examination of the stamens is necessary for determination.

a. Leaflets small and narrow (5–11 mm. long and about 2 mm. wide), numerous (9–50 pairs per pinna).
  b. Leaflets less than 30 pair per pinna, pubescent; mature peduncles 2–3 cm. long; flowers relatively large (calyx about 2.5 mm. long)..... 1. A. CARBONARIA
  bb. Leaflets usually 30 or more pairs per pinna, glabrous; peduncles less than 1.5 cm. long; flowers small (calyx about 1 mm. long)..... 2. A. CARIBAEA
aa. Leaflets larger and broader (mostly 15–40 mm. long and 10–20 mm. wide), few or several (2–9 pairs per pinna).
  b. Leaflets tapered and bluntly acute apically; flowers sessile..... 3. A. ADINOCEPHALA
  bb. Leaflets obtuse or rounded to emarginate apically; flowers pedicellate.
    c. Flowers all alike, short-pedicellate (pedicels mostly about 2 mm. long); mature leaflets, young twigs, and legume sparingly pubescent or glabrous..... 4. A. LEBBECK
    cc. Flowers dimorphic, all except center one long-pedicellate (pedicels 8–15 mm. long); mature leaflets, young twigs, and legume tomentose to moderately pubescent..... 5. A. LONGEPEDATA

1. ALBIZZIA CARBONARIA Britton ex Britt. & Wils., Scientif. Surv. Porto Rico & Virgin Isl. 6:348. 1926.

Albizzia malacocarpa Standl. ex Standl. & Cald. Fl. Salv. 96. 1925 (hyponym); Britt. & Rose, in N. Am. Fl. 23:44. 1928, fide Britt. & Killip.

Moderate or large tree, the branchlets tomentose when young becoming glabrous, moderately lenticellate, unarmed. Leaves moderately large, bipinnate, the pinnae 7–15 pairs opposite on the rachis, the leaflets 10–25 pairs per pinna; petioles mostly 2–3 cm. long, tomentulose, nearly terete, usually eglandular; primary rachis up to 10 cm. long, similar to the petiole, bearing at the apex at insertion of terminal pair of pinnae a sessile, subcupular gland; pinnular rachis 2–5 cm. long, puberulent, usually bearing a sessile gland at insertion of the terminal pair of leaflets; leaflets opposite, oblong-subfalcate, 4–6 mm. long and 1–2 mm. wide, asymmetrically acute apically, obliquely rounded or subtruncate basally, pubescent above and more heavily so below, somewhat paler below, the costa excentric, the venation obscure; stipules early caducous. Inflorescence of several pedunculate umbels from terminal and subterminal defoliate or minutely foliate nodes; peduncles slender, up to 3 cm. long, tomentulose; bractlets linear-spatulate, caducous. Flowers briefly pedicellate, dense; calyx narrowly obconic, about 2.5 mm. long, tomentulose; corolla narrowly funnelform, about 5 mm. long, tomentose, the lobes ½ the length of the tube; stamens about 14 mm. long, the staminal tube well included; ovary glabrous. Legume broadly linear, 8–11 cm. long and almost 2 cm. wide, stipitate, pubescent, falsely septate, the seeds transverse.

Salvador, Panama, and Colombia.

DARIÉN: Cana, *Williams 952.*

A. malacocarpa was described in part (flowers) from a Panama specimen *(Williams 952)*. On the basis of certain characteristics *A. carbonaria* might well be considered *Pithecolobium* (or *Samanea*, if this be recognized as distinct from *Pithecolobium*) instead of *Albizzia*. Yet the legume better fits *Albizzia*.

2. ALBIZZIA CARIBAEA (Urban) Britt. & Rose, in N. Am. Fl. 23:44. 1928.

Pithecolobium caribaeum Urban, Symb. Ant. 2:260. 1900.

Moderate to tall tree, the branchlets puberulent or almost glabrous, inconspicuously lenticellate. Leaves large, bipinnate, the pinnae 5–10 pairs, opposite, the leaflets 30–50 pairs; petiole 1–5 cm. long, terete except sulcate above, more or less puberulent, bearing above near the middle an orbicular gland concave above; rachis up to 18 cm. long, similar to the petiole, frequently glandular at the upper 1 to few rachial nodes; pinnular rachis about 6 cm. long, similar, eglandular; leaflets inequilaterally linear, 5–11 (usually 7–8) mm. long and 1–2 mm. wide, subtruncate and oblique basally, asymmetrically obtuse apically, glabrous, the costa excentric; stipules caducous or lacking. Inflorescence of subterminal, axillary, pedunculate heads; peduncles short, 6–15 mm. long, pubescent or subglabrous; heads globose, the bracts minute. Flowers small, pink, sessile; calyx turbinate, about 1 mm. long, puberulent-pilosulous; corolla funnelform, about 4 mm. long, subglabrous; stamens about 1 cm. long, the staminal tube included; ovary glabrous or shortly pilose apically, several ovulate. Legume linear, usually about 10 cm. long and 1.5–2.5 cm. wide, straight, flat and thin, the margins elevated, glabrous or subglabrous, transversely striate, the seeds transverse.

West Indies; north coast of South America, and lower Central America.

SAN BLAS: Puerto Obaldía, *Pittier 4326.*

This species is distinguished from most species of the genus in Panama by the fine "fern-like" foliage and short-pedunculate heads. Unless in fruit it is easily mistaken for *Enterolobium:* however, the leaflets are somewhat larger than is the case with *E. Schomburgkii* and somewhat smaller than is usual for *E. cyclocarpum*, the only two species of *Enterolobium* occurring in Panama.

3. ALBIZZIA ADINOCEPHALA (Donn. Smith) Britt. & Rose ex Record in Trop. Woods 10:22. 1927.

Pithecolobium adinocephalum Donn. Smith, in Bot. Gaz. 57:419. 1914.
Pithecolobium discolor Pittier, in Contr. U. S. Nat. Herb. 20:464. 1922, not Britton.

Large forest tree, the branchlets glabrous except at the extreme tips and somewhat corky or irregular. Leaves large, bipinnate, the pinnae (1) 2–3 pairs opposite on the rachis, the leaflets (2) 3–4 (5) pairs per pinna; petiole slender, 2–8 cm. long, terete, glabrous or lightly puberulent, swollen basally, bearing a longitudinally elongate, concave gland sunken in the upper surface of the petiole below the middle; primary rachis similar to the petiole, eglandular, longitudinally sulcate above; pinnular rachis similar, except bearing glands like that of the petiole at the upper pinnular nodes; leaflets opposite, ovate-lanceolate to ovate-elliptic, mostly 2–4 cm. long and 1–2 cm. wide, bluntly acute apically, mostly obtuse basally, dull and lightly puberulent above, lighter and puberulent below, the veins very prominent and reticulate above; stipules apparently lacking. Inflorescence a terminal or subterminal panicle, the ultimate divisions capitate from slender, puberulent,

ebracteolate peduncles; heads several-flowered, dense, minutely bracteolate. Flowérs small, white, fragrant; calyx funnelform, little more than 1 mm. long, silvery-pubescent above, the teeth small; corolla funnelform, about 3 mm. long, puberulent or subglabrous, the teeth as long as the tube; stamens many, about 1 cm. long, glabrous, the staminal tube about equalling the corolla; ovary glabrous. Legume broadly linear, 10–17 cm. long and 1.5–2.0 cm. wide, flat and thin, glabrous, transversely striate, dehiscent, 10- to 13-seeded.

British Honduras and Salvador to Panama.

CANAL ZONE: Ancón, *Pittier 5737*; Balboa, *Standley 26045*. PANAMÁ: Culebra Island, *Hayes 28*; sterile specimens from Standley afford many other records from the Canal Zone and nearby Panama.

A fairly common tree of Central America, much resembling certain species of *Leucaena*.

4. ALBIZZIA LEBBECK (L.) Benth. in Hook. Lond. Jour. Bot. 3:87. 1844.

Mimosa Lebbeck L. Sp. Pl. 516. 1753.
Mimosa speciosa Jacq. Ic. Pl. Rar. 1:19, *pl. 198*. 1786.
Acacia Lebbeck Willd. Sp. Pl. 4:1066. 1806.
Feuilléa Lebbeck Ktze. Rev. Gen. Pl. 1:184. 1891.

Many additional synonyms are given by Bentham (Trans. Linn. Soc. 30:562. 1875) for this Old World species.

Small or moderate, spreading tree, the branchlets puberulent when young soon becoming glabrous, conspicuously white-lenticellate. Leaves moderately large, mostly bipinnate, the pinnae 2–4 pairs opposite on the rachis, the leaflets 4–9 pairs; petiole 2–10 cm. long, glabrous, bearing on the upper side below the middle a sessile, oblong, concave gland; primary rachis similar to the petiole, sulcate above, often bearing a sessile, scutelliform gland at insertion of the upper pair of pinnae; pinnular rachis similar, bearing at or just below the upper 2–3 rachial nodes glands like the gland of the petiole; leaflets opposite, asymmetrically oblong, 2–4 cm. long and mostly 1–2 cm. wide, rounded-subtruncate to obtuse apically, obtuse and very inequilateral basally, essentially glabrous above and below. Inflorescence of many long-pedunculate umbels axillary from the subterminal nodes (2–3 per node); peduncles 3–10 cm. long, sparingly puberulent; umbels dense, globose, the pedicels mostly about 2 mm. long, the bractlets minute. Flowers cream-colored, fragrant; calyx funnelform, about 4 mm. long, unequally toothed or cleft, golden-tomentulose apically; corolla funnelform, 6–7 mm. long, puberulent, the teeth prominent; stamens many, as much as 3 cm. long, glabrous, the staminal tube well included; ovary glabrous. Legume broadly linear or narrowly oblong, usually 15 or more cm. long and 3–5 cm. wide, very thin and dry, glabrous, thinly margined, transversely striate; seeds few, transverse.

Native to Africa and Asia, introduced into various parts of the New World tropics.

CANAL ZONE: Colón, *Pittier 6672*.

The popular name "woman's tongue" is given this species. It is quite common in the West Indies, more so than on the Central American mainland. In fruit it may be confused with species of *Leucaena*.

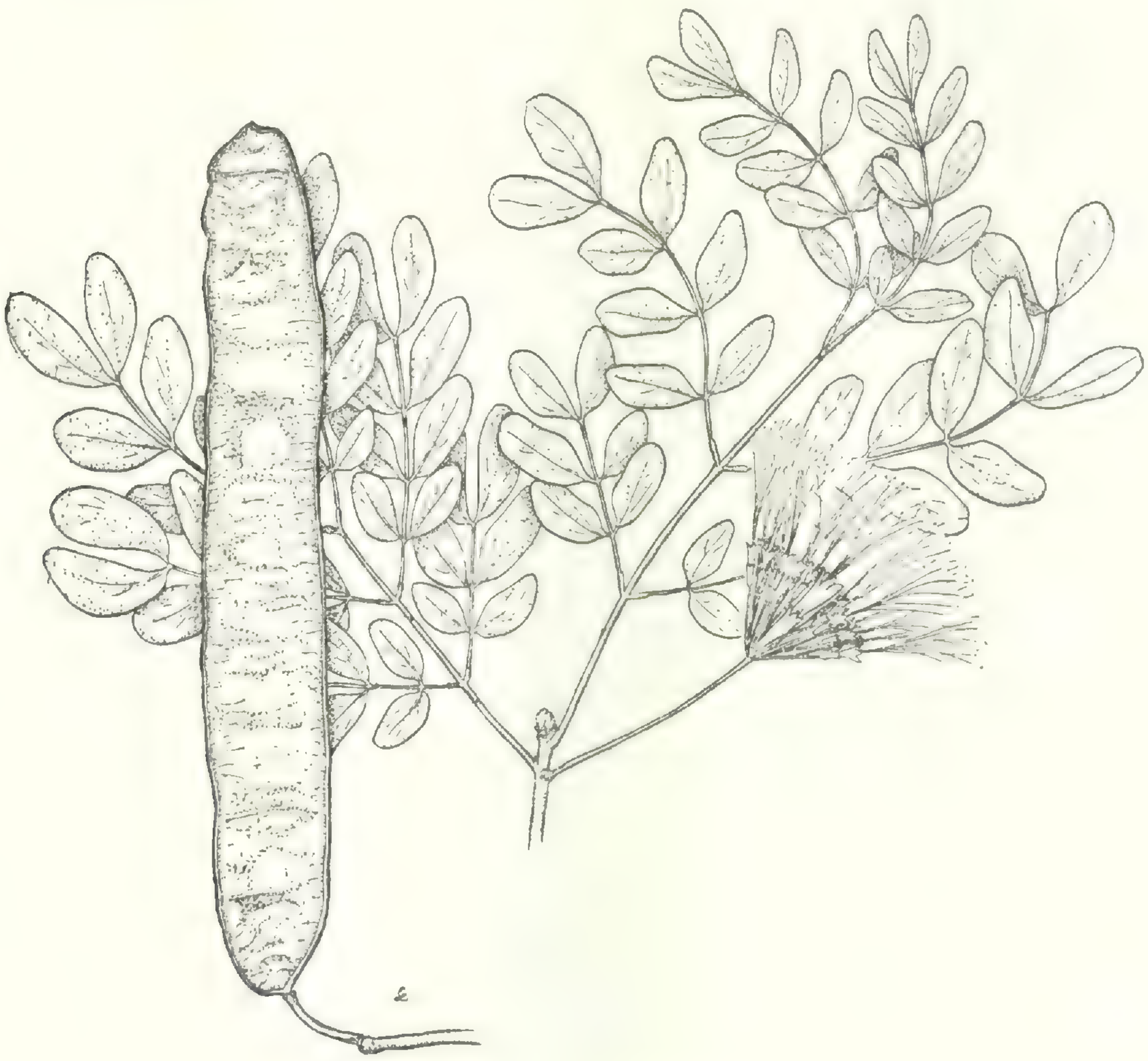

Fig. 94. *Albizzia longepedata*

5. ALBIZZIA LONGEPEDATA (Pittier) Britt. & Rose, ex Record in Trop. Woods 11:14. 1927.

Pithecolobium longepedatum Pittier, in Contr. U. S. Nat. Herb. 20:464. 1922.
Samanea Samanigua Pittier, in Bol. Cient. y Tecn. Mus. Com. Venez. 1:54. 1925.

Large tree, the young branchlets brownish-tomentose. Leaves large, bipinnate, the pinnae 2–6 (usually 3–4) pairs opposite on the rachis, the leaflets 3–7 pairs per pinna; petioles usually 3–4 cm. long, brownish-tomentose, bearing a sessile, concave, patelliform gland on the upper side near or slightly above the middle; rachis 3–15 cm. long, similar to the petiole, often with sessile, concave glands at or below insertion of the pairs of pinnae; pinnular rachis similar, bearing small glands below the rachial nodes; leaflets ovate to obovate, 15–40 mm. long and 10–25 mm. wide, rounded to subcuneate and somewhat oblique basally, rounded or emarginate apically, opposite, softly pubescent above and more densely so below, the venation

prominent above; stipules linear, caducous. Inflorescence of pedunculate umbels axillary from the subterminal nodes (1–3 per node); peduncle 3–9 cm. long, brownish-tomentose; pedicels slender, 8–15 mm. long, tomentose; bractlets linear, slender, early caducous. Flowers whitish, in many-flowered umbels, dimorphic, the central flower sessile and gross; calyx funnelform, 6–7 mm. long (tubular and 10–12 mm. long in central, sessile flower), tomentose; corolla funnelform, about 10 mm. long (tubular and 20–25 mm. long in central, sessile flower), tomentose, the teeth prominent and acute; stamens about 35 mm. long, the staminal tube included; ovary pubescent. Legume broadly linear, 15–20 cm. long and 2.5–3.5 cm. wide, pubescent, tardily dehiscent, the seeds several, transverse.

Salvador and Guatemala to northern South America.

CANAL ZONE: R. Pequení, *Steyermark & Allen 17155.*

This species is quite distinct from other species of *Albizzia* in Panama, differing primarily by its pronouncedly umbellate, long-pedicellate flowers.

5. CALLIANDRA Benth.

CALLIANDRA Benth. in Hook. Jour. Bot. 2:138. 1840, nom. conserv.

Anneslia Salisb. Parad. Lond., *pl. 64.* 1807.
Inga Annesleya G. Don, Gen. Hist. Dichl. Pl. 2:396. 1832, in part.
Clelia Casar. Nov. Stirp. Brasil. Dec. 83. 1845.
Codonandra Karst. Fl. Columb. 2:43, *t. 122.* 1862.

Usually shrubs or small trees, unarmed except in one or two (non-Panamanian) species, mostly not heavily pubescent. Leaves bipinnate, the pinnae 1 to several pairs; leaflets 1 to many pairs per pinna; petiole and rachis eglandular; leaflets large and broad (ovate) or more frequently small and narrow (linear or linear-oblong), glabrous in most species, frequently ciliate marginally, almost invariably very oblique basally, the costa prominent, but the secondary veins obscure in many species; stipules mostly striate and subpersistent. Inflorescence commonly of axillary, pedunculate spikes, sometimes a terminal raceme or panicle. Flowers in dense, globose heads, sometimes dimorphic (center flower of head larger or more gross, sometimes sterile), normally 5-parted and perfect, regular, sympetalous; calyx relatively broad, mostly cupulate or campanulate; corolla usually funnelform, never narrow and tubular like species of *Inga* and *Pithecolobium,* usually lobed for about half its length, the lobes valvate; stamens many, elongate, conspicuous and showy, obscuring the corolla, united below into an included or exserted staminal tube; anthers small, usually eglandular; ovary usually sessile, glabrous, several-ovulate, the style filiform, the stigma terminal. Legume broadly linear, straight or nearly so, gradually constricted baseward and thus cuneate-substipitate, flat and thin, the margins elevated, bivalvate, the valves elastically dehiscent from the apex but not twisting, not septate, the seeds (obliquely) transverse or nearly longitudinal.

Primarily a New World genus, extending from southwestern United States and Mexico to southern South America: one or two Oriental or African species have

at times been recognized.

The genus is fairly distinctive and seemingly quite natural. It is especially characterized by the glandless petiole and rachis, the dense heads of "exserted stamens" and the distinctive, elastically dehiscent legume. Specific boundaries within the genus are for the most part indistinct and often artificial. Several readily identifiable complexes can be distinguished, and within these a great many of the species can be united with profit. Probably not more than 20 or 25 "good" species occur in all Central America, most of these in the northern part. Eight species are here recognized from Panama, one of which is questionably recorded.

a. Leaflets normally 3 per pinna, comparatively large and broad (about 1 cm. wide); pinnae 1 pair.
  b. Flowers large (corolla about 13 mm. long, stamens 6–7 cm. long); staminal tube well exserted (about 4 cm. long); peduncles thick..... 1. C. GLABERRIMA
  bb. Flowers smaller (corolla about 6 mm. long, stamens 2–2.5 cm. long); staminal tube included; peduncles slender..... 2. C. SEEMANNI
aa. Leaflets few to many per pinna, comparatively small (never more than a few mm. wide); pinnae 1 to several pairs.
  b. Inflorescence of axillary, pedunculate heads; pinnae 1–11 pairs.
    c. Pinnae a single pair..... 3. C. MAGDALENAE
    cc. Pinnae 2–11 pairs.
      d. Corolla essentially glabrous; leaflets membranaceous, dull, the secondary veins obscure.
        e. Branchlets terete; flowers rather small..... 4. C. CARACASANA
        ee. Branchlets quadrangular, markedly angled; flowers larger..... 5. C. TETRAGONA
      dd. Corolla pubescent; leaflets thicker, often subcoriaceous, darker or more lustrous above, venation more or less evident as far as known.
        e. Pinnae 2–6 pairs; leaflets usually 10–25 pairs, 4–7 mm. long; corolla about 8 mm. long..... 6. C. CUMINGII
        ee. Pinnae mostly 7–11 pairs; leaflets normally 20–65 pairs, mostly 3–5 mm. long; corolla 5–6 mm. long..... 7. C. PITTIERI
  bb. Inflorescence a terminal raceme or panicle; pinnae several to many (usually about 15) pairs..... 8. C. CONFUSA

1. CALLIANDRA GLABERRIMA (Benth.) Britt. & Killip, in Ann. N. Y. Acad. Sci. 35:134. 1936.

Calliandra glyphoxylon var. *glaberrima* Benth. in Trans. Linn. Soc. 30:539. 1875.

Small tree or shrub?, the branchlets essentially glabrous, striate, callous but hardly lenticellate. Leaves moderately small, bipinnate, the pinnae only 1 pair, the leaflets 3 (2–4?) per pinna; petioles mostly 1–2 cm. long, subglabrous, sulcate above, eglandular, apiculate apically from the lower side; pinnular rachis similar to the petiole; leaflets oblong-falcate, the terminal pair mostly 2–4 cm. long and about 1 cm. wide, the lower leaflet usually half or less this size, blunt or bluntly acute apically and minutely mucronulate, very obliquely obtuse or rounded basally, glabrous and lustrous above and below, sparingly ciliate on the margins, the 2–3 main veins palmate, smaller veins conspicuously reticulate, coriaceous; stipules ovate, 1–2 mm. long, longitudinally striate, subpersistent. Inflorescence of axillary, pedunculate heads; peduncles about 1 cm. long; heads dense; bracts more or less ovate, little more than 1 mm. long, persistent. Flowers large, red; calyx campanulate, 2–3 mm. long, striate, glabrous, the teeth short and broad; corolla funnel-

form, about 13 mm. long, glabrous; stamens as much as 6–7 cm. long, united below into a glabrous staminal tube often about 4 cm. long, thus strongly exserted; ovary glabrous, tapered basally. Legume typical of the genus.

Colombia and Panama.

CANAL ZONE: R. Indio, *Dodge & Allen 17370.* COCLÉ: Bismarck, *Williams 141.* PANAMÁ: north of Panama City, *Bro. Paul 612.*

A few South American species, including *C. carbonaria,* are similar to our Panamanian specimens, and with additional collections may possibly prove to grade into this species and/or into one another. Knowing how variable species in this group may be, we have refrained from describing as new the *Dodge & Allen 17370* specimen cited, even though its flowers are considerably larger than is typical for *C. glaberrima* or other related species examined. The description here given is taken mostly from the *Dodge & Allen 17370* specimen and is not necessarily "typical" of *C. glaberrima.*

C. glaberrima is allied to the well-known *C. emarginata* of northern Central America and Mexico, and to other species of Britton & Rose's TERGEMINAE. The TERGEMINAE as constituted by Britton and Rose is a highly unworkable complex of doubtful entities. Seemingly it should be condensed into a half-dozen or less species. In spite of marked variability in the species, none of the Mexican or Central American ones possess flowers nearly so large as those of our Panamanian citation.

C. glaberrima, along with *C. Seemanni* and its extra-Panamanian allied species, are easily distinguished from all other species of *Calliandra* in Panama by the bipinnular, few-foliolate leaves with relatively large leaflets. Larger flowers and extremely exserted staminal tube serve readily to distinguish *C. glaberrima* from *C. Seemanni.*

2. CALLIANDRA SEEMANNI Benth. in Seem. Bot. Voy. Herald, 116, *pl. 22.* 1853.

Feuilléea Seemanni Ktze. Rev. Gen. Pl. 1:189. 1891.
Anneslia Seemanni Britt. & Rose, in N. Am. Fl. 23:54. 1928.

Large shrub or small tree?, the branchlets glabrous or lightly canescent-puberulent. Leaves moderately small, bipinnate, the pinnae a single pair, the leaflets 1 pair (plus a third smaller leaflet below to the outside) per pinna; petiole slender, up to 2 cm. long, essentially glabrous, sulcate above, eglandular, apiculate from below terminally; pinnular rachis similar to the petiole; leaflets obliquely oblong, mostly 2–4 cm. long and about 1–1.5 cm. wide, obtuse to acute apically, rounded and very inequilateral basally, with one chief nerve and two smaller nerves palmate from the base, the secondary venation reticulate, glabrous except usually ciliolate on the margin; stipules lanceolate, small. Inflorescence of axillary, pedunculate heads; peduncles slender, mostly 2–3 cm. long; heads several-flowered, globular; floral bracts lanceolate, subpersistent. Flowers dense; calyx narrowly cupulate, about 2 mm. long, glabrous, striate, the teeth prominent; corolla funnelform,

about 6 mm. long, glabrous; stamens 2–2.5 cm. long, united below into an included staminal tube. Legume broadly linear, up to 10 cm. long and about 1 cm. wide, glabrous, the few brown seeds reported white-dotted.

Reported from northern South America (erroneously from Colombia, fide Britton & Killip); Costa Rica?.

The species is based upon a Seemann collection from Veraguas, Panama. The type (the only Panamanian record) has not been available for examination, but is well illustrated with the original description: it is strongly suspected that the species is merely a variant of the older *C. emarginata* (which in turn is probably scarcely separable from *C. tergemina*), and incorporation under one of these names may eventually be in order. As mentioned under discussion of *C. glaberrima*, it seems impossible to accept Britton & Rose's inordinate splitting of the TERGEMINAE, into which section the doubtfully distinct *C. Seemanni* falls.

3. CALLIANDRA MAGDALENAE (Bert.) Benth. in Lond. Jour. Bot. 5:102. 1846.

Acacia Magdalenae Bert. ex DC. Prodr. 2:455. 1825.
Feuilléea Magdalenae Ktze. Rev. Gen. Pl. 1:188. 1891.
Calliandra riparia Pittier, Arbol. y Arbust. Legum. Dec. 6–8:80. 1927.
Anneslia Magdalenae Britt. & Rose, in N. Am. Fl. 23:60. 1928.
Anneslia Tonduzii Britt. & Rose, loc. cit. 61. 1928.
Anneslia chiapensis Britt. & Rose, loc. cit. 1928.
Calliandra Schultzei Harms, in Fedde Rep. Sp. Nov. 24:209. 1928.
Calliandra Tonduzii Standl. in Field Mus. Publ. Bot. 4:309. 1929.
Calliandra angustidens Britt. & Killip, in Ann. N. Y. Acad. Sci. 35:134. 1936.

Tree to 10 m. tall, the branchlets somewhat ascending-pubescent when young, becoming glabrous in age. Leaves moderate, bipinnate, the pinnae 1 pair, the leaflets several (usually 10–20) per pinna; petiole short, about 1 cm. long, terete, tomentulose, eglandular, bearing terminally an apicule from the lower side; pinnular rachis 5–9 cm. long, ridged and tomentose above; leaflets linear-ovate or linear-lanceolate to linear-oblong, mostly about 1 cm. long and 3 mm. wide, broadly acute or sometimes obtuse apically and minutely mucronulate, obliquely truncate basally, glabrous above and below, lustrous above, often ciliate, the costa slightly excentric, 1–2 minor veins palmate from the base, secondary veins prominently reticulate; stipules lanceolate, 3–6 mm. long, striate, subpersistent. Inflorescence of axillary, pedunculate heads; peduncles about equalling petioles, puberulent; floral bracts lanceolate, quite small, persistent. Flowers rose-red, several in dense globular heads; calyx funnelform-campanulate, about 2 mm. long, glabrous, striate; corolla funnelform, 5–7 mm. long, glabrous, the lobes prominent; stamens in age 2.5 or more cm. long, the staminal tube about equalling the corolla. Legume linear-oblong, reported up to 14 cm. long and about 1 cm. wide, pubescent when young, said to be (erroneously?) glabrous at maturity.

As here interpreted (broadly), southern Mexico, Central America to northern South America.

CHIRIQUÍ: Progreso, *Cooper & Slater 318;* Remedios, *Allen 3666;* San Felix, *Allen 1958;* R. Tinta, *Woodson, Allen & Seibert 401.* VERAGUAS: Soná, *Allen 1040.*

While the species assumes a fairly constant form in Panama, it grades into a number of variants in northern Central America and Mexico, and in northern South America. As a result numerous bipinnular "species" have been described which are nearly impossible to delimit precisely. South American (Colombian) specimens taken by Britton & Killip to be *C. Magdalenae* may appear quite different from those of northern Central America and even Panama. On the other hand, there seems little doubt that the Colombian *C. Schultzei* is the same species as our Panamanian citations. Yet Bentham cites a Seemann collection (as being *C. Magdalenae*) from the same province as the *Allen 1040* collection. With uncertainty as to the exact boundaries of *C. Magdalenae*, a few possible and probable synonyms have been combined for practical reasons under the oldest name. Should *C. Schultzei* in reality be distinct from *C. Magdalenae*, both it (on the basis of recent collections) and *C. Magdalenae* (solely on the basis of Bentham's citation) would have to be considered as occurring in Panama.

4. CALLIANDRA CARACASANA (Jacq.) Benth. in Trans. Linn. Soc. 30:543. 1875.

Mimosa caracasana Jacq. Coll. 4:142. 1790.
Acacia caracasana Willd. Sp. Pl. 4:1068. 1806.
?Calliandra portoricensis Benth. in Hook. Lond. Jour. Bot. 3:99. 1844. (For numerous synonyms to this species see Benth. in Trans. Linn. Soc. 30:543. 1875.)
Feuilléea caracasana Ktze. Rev. Gen. Pl. 1:187. 1891.
Anneslia caracasana Britt. & Rose, in N. Am. Fl. 23:65. 1928.
Calliandra Toroana Britt. & Rose, in Ann. N. Y. Acad. Sci. 35:137. 1936.

Shrub or weak slender tree, the branchlets puberulent to glabrous. Leaves moderately large, bipinnate, the pinnae 2–6 (mostly 4–5) pairs, the leaflets 10–35 pairs; petiole slender, 1–3 cm. long, glabrous or nearly so, eglandular; rachis mostly 3–4 cm. long, similar to the petiole, bearing a terminal apicule from the lower side; pinnular rachis up to 7 cm. long, glabrous except frequently puberulent above; leaflets linear or linear-oblong and more or less straight, mostly 6–8 mm. long and about 1 mm. wide, obtuse or somewhat acute apically, asymmetrically rounded or subtruncate basally, glabrous (in age) or pubescent, dull above and below, the costa somewhat excentric, other veins obscure; stipules lanceolate, 3–6 mm. long. Inflorescence of axillary, pedunculate heads; peduncles slender, 2–5 cm. long or even longer, glabrous or puberulent; floral bracts minute, usually ciliate; head small, several-flowered, globular. Flowers whitish or pinkish; calyx funnelform-campanulate, scarcely more than 1 mm. long, subglabrous; corolla broadly funnelform, little more than 2 mm. long, glabrous or subglabrous; stamens about 16 mm. long, the staminal tube included. Legume broadly linear, about 8 cm. long and almost 1 cm. wide, constricted basally, glabrous or lightly puberulent.

Venezuela to Ecuador; Panama. "Species" probably conspecific with *C. caracasana* if broadly regarded, occur in Mexico, northern and middle Central America and the West Indies.

CHIRIQUÍ: R. Chiriquí Viejo, *P. White 342*.

The *White 342* specimen cited (fruit only) is in rather poor condition. It seems identical with *C. tetragona* and logically should be cited as *C. tetragona*, except for the absence of the characteristic stem angulations, a character possibly of little genetic weight. Even if this specimen be regarded as *I. tetragona*, the entity represented by *C. caracasana* is to be expected in Panama. *C. portoricensis* has been distinguished from the usually slighter *C. caracasana* in reportedly having white stamens while the latter has pink, red, or purple stamens. This characteristic, in view of morphological intergradation, seems of dubious value for specific distinction. Bentham himself states (Trans. Linn. Soc. 30:543. 1875) concerning *C. caracasana:* "The six preceding species [*C. portoricensis* is the first preceding one and *C. tetragona* the first subsequent one], however, are very closely allied to each other, and might almost be classed as varieties of a single species." Monographic work is sorely in need here and will likely show a widespread, variable complex centered in these tropical American species, in which speciation has not as yet segregated clear-cut entities.

5. CALLIANDRA TETRAGONA (Willd.) Benth. in Hook. Lond. Jour. Bot. 2:139. 1840.

Acacia tetragona Willd. Sp. Pl. 4:1069. 1806.
Mimosa quadrangularis Poir. in Lam. Encycl. Meth. Suppl. 1:72. 1810.
Acacia quadrangularis Link, Enum. Hort. Berol. 2:445. 1822.
Anneslia tetragona Donn.-Smith, Enum. Pl. Guat. 1:10. 1889.
Feuillëea tetragona Ktze. Rev. Gen. Pl. 1:189. 1891.
Calliandra portoricensis var. *multijuga* Micheli, in Bot. Gaz. 20:285. 1895, fide Britt. & Rose.

Shrub or small tree, the branchlets puberulent when young becoming glabrate, usually markedly quadrangular, longitudinally striate, scarcely lenticellate. Leaves moderately large, bipinnate, the pinnae 4–8 pairs opposite on the rachis, the leaflets 15–35 pairs per pinna; petiole mostly 2–3 cm. long, puberulent or subglabrous, angled, somewhat sulcate or ridged above, eglandular; rachis similar to the petiole, often bearing tufts of hair at insertion of the pinnae; pinnular rachis 3–8 cm. long; leaflets linear to linear-oblong, nearly straight, mostly about 8 mm. long and little more than 1 mm. wide, obtuse or somewhat acute apically, asymmetrically rounded to truncate basally, glabrous or ciliate on the margin, dull above and below, the costa somewhat excentric, the other veins obscure; stipules narrowly lanceolate, about 6 mm. long, striate, subpersistent. Inflorescence of 1 to few pedunculate heads from the upper axils, the terminal and subterminal nodes frequently defoliate; peduncles elongate, not uncommonly 7–8 cm. long in age, similar to the petiole; heads dense, several-flowered, globular; floral bracts minute. Flowers white; calyx funnelform-campanulate, about 2 mm. long, subglabrous, the teeth acute; corolla funnelform, about 6 mm. long, glabrous; stamens 3 cm. long or longer, the staminal tube included. Legume up to 12 cm. long and about 1 cm. wide, glabrous, otherwise typical of the genus.

Southern Mexico to northern South America.

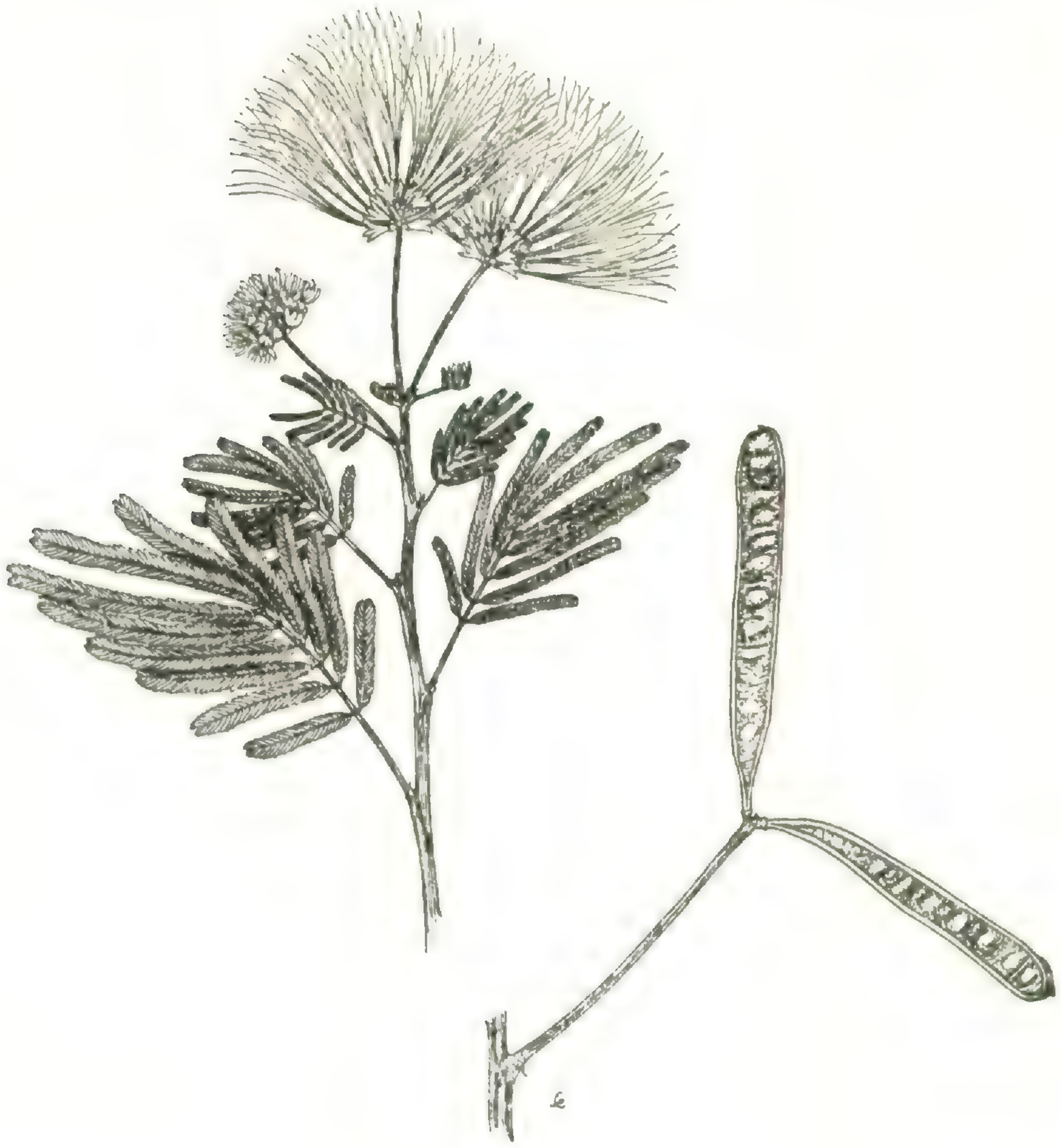

Fig. 95. *Calliandra tetragona*

CHIRIQUÍ: Boquete, *Pittier 3140;* Hato del Jobo, *Pittier 5423.* COCLÉ: El Valle, *Allen 3819; Hunter & Allen 357.*

This species is distinguished, perhaps somewhat "unnaturally," by the tetragonal branchlets. Certainly some species normally identified as *C. portoricensis* or *C. caracasana* seem identical with *C. tetragona* except for the angled stem. It may be that a single or few-gene characteristic (angled stem) has appeared throughout the range of what might be called the *C. caracasana-C. portoricensis* complex. Yet this character is sufficient to distinguish (somewhat arbitrarily) this species from others of the genus.

6. CALLIANDRA CUMINGII Benth. in Hook. Jour. Bot. 2:140. 1840.

Inga speciosa Mart. & Gal. in Bull. Acad. Brux. 10^2:320. 1843?, fide Ind. Kew.
Feuilléea Cumingii Ktze. Rev. Gen. Pl. 1:187. 1891.
Anneslia Cumingii Britt. & Rose, in N. Am. Fl. 23:57. 1928.

Shrub, the branchlets puberulent or lightly pubescent, becoming glabrous in age. Leaves moderately small, bipinnate, the pinnae usually 2–3 pairs opposite on the rachis, the leaflets several to many pairs per pinna; petiole usually less than 1 cm.

long, lightly pubescent, eglandular; rachis 5–20 mm. long similar to the petiole, eglandular, bearing a terminal apicule from the lower side; pinnular rachis slender, up to 2 cm. long, puberulent, eglandular; leaflets linear-oblong or narrowly oblong, usually 4–7 mm. long and 1–2 mm. wide, blunt or obtuse and often minutely mucronate apically, obliquely rounded or subtruncate basally, sparsely pubescent or subglabrous, the costa slightly excentric, the venation fairly prominent below, somewhat lighter in color and duller below than above; stipules small, lanceolate-subulate. Inflorescence of pedunculate heads solitary or rarely geminate in the upper axils; peduncles 2–3 cm. long, lightly pubescent; floral bracts small, puberulent. Flowers in compact, several-flowered heads, pubescent or lightly pilose apically, purplish; calyx campanulate, 1–2 mm. long, pubescent on the teeth; corolla funnelform, about 8 mm. long, lightly pubescent with long hairs, the lobes about ⅓–¼ the length of the tube; stamens about 2.5 cm. long, the staminal tube mostly included; ovary glabrous. Legume linear, up to 8 cm. long and about 8 mm. wide, puberulent?, dehiscent as typical of the genus.

Panama, Mexico?, northern South America?

PROVINCE UNKNOWN: without locality, *Cuming 1248*.

The species was described from a Panamanian collection by Cuming *(1248)*, which we have not had opportunity to examine. No later collections from Panama have come to our attention. Bentham regarded Mexican and Venezuelan material as conspecific with *C. Cumingii,* but Britton and Rose have regarded the species as confined to Panama. The above description is pieced together from various incomplete descriptions of the species and certain herbarium sheets that presumably are (or are very similar to) *C. Cumingii.*

7. CALLIANDRA PITTIERI Standl. in Contr. U. S. Nat. Herb. 18:104. 1916.

Calliandra bella var. *Trianae* Benth. in Trans. Linn. Soc. 30:556. 1875.
Calliandra Lehmanii Harms, in Fedde Rep. Sp. Nov. 17:90. 1921.
Anneslia Pittieri Britt. & Rose, in N. Am. Fl. 23:63. 1928.

Small tree with flat crown, the branchlets sparingly appressed-pubescent or puberulent when young, becoming glabrous. Leaves moderate, bipinnate, the pinnae mostly 7–11 pairs opposite on the rachis, the leaflets several or many (20–65 pairs); petiole short, normally less than 1 cm. long, terete, puberulent, eglandular; rachis up to 9 cm. long, similar to the petiole; pinnular rachis 2–5 cm. long; leaflets small, linear or linear-oblong, 3–5 mm. long and less than 1 mm. wide, acute to obtuse apically, inequilaterally rounded basally, usually minutely ciliolate but otherwise glabrous, the costa conspicuous and somewhat excentric, more or less lustrous on the upper surface; stipules linear-lanceolate, about 3 mm. long, persistent. Inflorescence of axillary, pedunculate heads; peduncles 1.5–4.5 cm. long, puberulent; heads few- to several-flowered, dense, spherical, the bracts small and subpersistent. Flowers red; calyx campanulate, little more than 1 mm. long, glabrous or puberulent, the teeth short and broad; corolla funnelform, 5–6 mm. long, pubescent; stamens about 3 cm. long, the staminal tube barely exserted.

Legume linear-spatulate, 5–8 cm. long and scarcely 1 cm. wide, pubescent, the margins thick.

Colombia and Panama.

DARIÉN: Caná, *Williams 707.*

This species, from a Colombian type *(Pittier 951)*, was recorded in the original description as occurring also in Panama (Caná, Darién, *Williams 707*). Britton and Rose, in the N. Am. Fl., so accepted its range. However, Britton and Killip (Ann. N. Y. Acad. Sci. 35:136. 1936) indicate that the Panamanian identification was in error, and that the species is in reality confined to Colombia. Morphologically, there seems little reason why the *Williams 707* specimen cannot be considered as *C. Pittieri,* and it is so listed here.

8. CALLIANDRA CONFUSA Sprague & Riley in Kew Bull. Misc. Inf. 1923:371. 1923.

Calliandra similis Sprague & Riley, loc. cit. 372. 1923.
Anneslia confusa Britt. & Rose, in N. Am. Fl. 23:70. 1928.
Anneslia similis Britt. & Rose, loc. cit. 71. 1928.

Small tree or shrub, the branchlets lightly hirsute to subglabrous, longitudinally striate. Leaves large, bipinnate, the pinnae 10–20 or more (usually about 15) pairs, opposite, the leaflets numerous (30–60, usually 40–50, pairs); petiole usually about 2 cm. long, pubescent to subglabrous, sulcate above, eglandular; rachis similar, 8–15 cm. long; pinnular rachis about 4 cm. long, ridged above, lightly pubescent; leaflets linear, usually about 5–6 mm. long and 1 mm. wide, acute or narrowly obtuse apically, obliquely truncate basally, glabrous above and below except appressed-ciliate on the margins, only the midvein prominent, this more or less central; stipules linear-lanceolate, 4–5 mm. long, glabrous, striate, caducous. Inflorescence a terminal raceme or panicle; peduncles mostly 5–8 mm. long, geminate or few-fasciculate, subglabrous; pedicels 2–4 mm. long; bracts lanceolate-caducous. Flowers in few-flowered umbels, purplish-red; calyx broadly campanulate, scarcely 2 mm. long, glabrous, 5-toothed, the teeth broad; corolla 5-lobed, cleft almost to the base, the lobes elliptic or oblong, 5–6 mm. long, glabrous, the tube about 1 mm. long; stamens as much as 6 cm. long, united below into a short staminal tube 2–3 mm. long; ovary glabrous. Legume almost 8 cm. long and about 1 cm. wide, strigose-pubescent, dehiscing as typical of the genus.

Panama to northern Central America and southern Mexico; northern South America?

CHIRIQUÍ: Boquete, *Terry & Terry 1637; Woodson & Schery 757;* R. Chiriquí Viejo, *G. & P. White 112; Allen 4651.*

This species is a member of the "Houstoniana complex" (HOUSTONIANAE of Britton and Rose) very common in Mexico and to a lesser extent in northern Central America. There are probably 3 or 4 tenable species in that area, of which *C. Houstoniana* dating from 1768 and *C. grandiflora* dating from 1788 are the best

Fig. 96. *Calliandra confusa*

known (*C. anomala* and *C. strigillosa* of the early 1800's may also be "good" species, but several additional "species" in this group, proposed by Britton and Rose and others, seem anything but clear-cut). The southern extension of this complex in Central America (Honduras to Panama) seems to be confined to the single species here listed. It is impossible to say without examining the type whether or not the earlier name, *C. calothyrsus* Meissn., for a South American specimen (collected in 1846 by Kegel in Surinam), can apply to the entity found in Panama.

In describing *C. confusa* and *C. similis*, Sprague and Riley seem to have hit upon two extremes of the same entity. Our cited specimens and others from Costa Rica to Guatemala appear to be quite intermediate between characteristics described for these names. Hence it has been necessary to regard *C. similis* as a synonym of *C. confusa*.

C. confusa is similar to *C. grandiflora*, but lacks the floral pubescence of that species. It is quite distinct from other species of *Calliandra* occurring in Panama, being the only species there having a terminal, racemose or paniculate type of inflorescence. The plant is very attractive because of the showy purplish-red flowers and fine foliage, and deserves attention as an ornamental.

6. ACACIA Willd.

Acacia Willd. Sp. Pl. 4:1049. 1806.

Numerous synonyms occur for the genus. Segregate genera proposed by Rafinesque (Sylva Tellur. 118–120. 1838) include: *Cuparilla*, *Drepaphyla*, *Eburnax*, *Esclerona*, *Gumifera*, *Hecatandra*, *Poponax*, *Senegalia*, and *Zigmaloba*. Britton and Rose segregates (N. Am. Fl. 23:85–96. 1928) include: *Acaciella*, *Acaciopsis*, *Bahamia*, *Fishlockia*, *Lucaya*, *Myrmecodendron*, *Tauroceras*, and *Feracacia* Britt. & Bro. Léon. Dalla Torre & Harms further list the following synonyms: *Arthosprion* Hassk.; *Chitonanthus* Lehm.; *Farnesia* Gasparr.; *Hoopesia* Buckl.; *Phyllodoce* Link; *Sassa* Bruce ex Gmelin; *Tetracheilos* Lehm.;*Vachellia* Wight & Arn.

Woody plants, usually armed with scattered thorns or stipular spines. Leaves (Central American species) bipinnate, the pinnae few or many, opposite, the leaflets mostly small and numerous; petiole in the majority of species bearing some sort of a gland or glandular field; rachis short or elongate, glandular or less often eglandular; stipules usually small and caducous but sometimes modified as prominent spines, in the "bull-horn" species these very large and myrmecophilous. Inflorescence basically of axillary, solitary or fasciculate, pedunculate heads, spikes, umbels or racemes, often appearing paniculate because of suppression of leaves at terminal and subterminal, floriferous nodes. Flowers small, usually numerous and dense, predominately whitish or yellowish, normally exceeding the bractlets; calyx usually campanulate, sympetalous, 4- or 5-toothed; corolla typically funnelform, sympetalous for most of its length or in some species 4- to 5-cleft nearly to the base; stamens diagnostic, numerous, free or rarely somewhat united at the extreme base; anthers small, rarely glandular; ovary small, the style and terminal stigma scarcely visible among the stamens. Legume usually oblong to linear, terete or more frequently compressed or flattened, usually straight, dehiscent and with slightly elevated margins, the seeds transverse.

Tropics and subtropics of New and Old Worlds, very prominent in Australia.

The genus is highly variable, with many groups of species simulating diverse other genera (parallel evolution) and reflecting environmental adaptation (xerophytism, etc.). It is thus extremely difficult to give a generalized yet definitive description for the genus (the numerous, free or nearly free stamens being the only binding characteristic), but it is even more difficult to establish clear-cut subdivisions of or within the genus. Most of the numerous segregates of *Acacia*, such as those recognized by Britton and Rose (N. Am. Fl. 23:84. 1928), depend upon subjective evaluation (viz.: coriaceous vs. cartilaginous; linear vs. oblong; subterete vs. turgid; promptly vs. tardily dehiscent; etc.). It becomes highly inconvenient with these segregates to determine the "genus," let alone the species,

except where perfect material (with fruit) and at least modest familiarity with the group is to be had. Even then many marginal cases exist, where a species may well fall into either of two "genera." Thus, for convenience, if nothing else, I prefer to recognize *Acacia* in the traditional broad sense, in spite of certain groups of species forming islands within the genus markedly different from other groupings of species.

The species of *Acacia* usually present considerable variability and intergradation. It would seem that formulation of species has been unusually inordinate in this genus. When material from Mexico to middle South America is examined and compared, or in areas from which abundant material is available, many specific distinctions fade. This appears especially true in the segregate genera "*Acaciella*" and "*Senegalia*" as considered by Britton and Rose. On the other hand, many of the "bull-horn" species, differing but difficult of separation, may prove constant with further collections. Collections of all species in Panama are rather meagre, with the possible exception of species occurring on Barro Colorado Island. It is as yet not possible to study degree of variation of these species within the country, nor to confidently correlate single or few collections with better known Mexican and northern Central American expressions of (presumably) the same entity.

a. Flowers pedicellate; petiole eglandular; twigs unarmed *("Acaciella")*.
  b. Leaflets nearly linear (about 6 mm. long and 1 mm. wide), numerous (frequently 60 or more pairs per pinna), subglabrous; twigs commonly subglabrous..... 1. A. ANGUSTISSIMA
  bb. Leaflets oblong or ovate (usually 8–9 mm. long and at least 2 mm. wide), fewer (9–25 pairs per pinna), pubescent; twigs often villous.... 2. A. VILLOSA
aa. Flowers sessile or subsessile; petiole with 1 or more glands; twigs rarely unarmed.
  b. Armament of scattered thorns or lacking; flowers whitish *("Senegalia")*.
    c. Flowers in short, oblong spikes, comparatively large..... 3. A. HAYESII
    cc. Flowers capitate, small.
      d. Leaflets relatively large (usually 10 mm. long), more or less oblong, pubescent at least below; thorns frequently lacking..... 4. A. GLOMEROSA
      dd. Leaflets small (usually 4–6 mm. long), linear or sublinear, glabrous except often ciliate marginally; thorns usually present.
        e. Costa of leaflet excentric, submarginal; petiolar gland usually solitary; legume glabrous or subglabrous in age..... 5. A. TENUIFOLIA
        ee. Costa of leaflet subcentral, at least apically; petiole frequently bearing 2 glands; legume tomentulose..... 6. A. RIPARIA
  bb. Armament of paired stipular spines; flowers yellowish.
    c. Stipular spines slender, usually whitish, solid, not ant-infested; peduncle not involucrate; in *A. farnesiana* older branchlets with axillary "cushions" or short-shoots, and the leaves small (scarcely 6 cm. long), with few pinnae.
      d. Leaves less than 6 cm. long, with 2–6 pairs of pinnae *("Vachellia")*..... 7. A. FARNESIANA
      dd. Leaves usually 10 cm. long or longer, with 8–60 pairs of pinnae *("Poponax")*. Not known from Panama outside of cultivation, but to be expected there..... 8. A. MACRACANTHA
    cc. Stipular spines mostly gross, dark, hollow, myrmecophilous; peduncle involucrate; leaves large (usually 1 dm. long or longer), with several pinnae ("*Myrmecodendron*" except no. 12).
      d. Inflorescence capitate; leaflets with a single prominent vein; leaf rachis glandular.
        e. Heads axillary; petiole eglandular..... 9. A. COOKII

ee. Inflorescence paniculate, the nodes not foliate; petiole bearing few to several glands..... 10. A. MELANOCERAS
dd. Inflorescence spicate; leaflets with 2–3 prominent veins; leaf rachis usually eglandular.
e. Legume turgid-compressed, dehiscent (often tardily), short-beaked, the pericarp thick; spike thin (about 3 mm. thick), without protruding bractlets; petiolar gland of 2–3 crateriform nectaries..... 11. A. COSTARICENSIS
ee. Legume terete, indehiscent, long-beaked, the pericarp thin; spike stout (almost 1 cm. thick), with protruding bractlets; petiolar gland with a solitary, crateriform nectary *("Tauroceras")*. To be expected in Panama..... 12. A. SPADICIGERA

1. ACACIA ANGUSTISSIMA (Mill.) Ktze. Rev. Gen. Pl. 3^2:47. 1898.

Mimosa angustissima Mill. Gard. Dict. ed. 8, no. 19. 1768.
Mimosa filicioides Cav. Icon. Pl. 1:55, *pl. 78*. 1791.
Acacia filicina Willd. Sp. Pl. 4:1072. 1806.
Mimosa ptericina Poir. in Lam. Encycl. Meth. Suppl. 1:74. 1810.
Acacia glabrata Schlecht. in Linnaea 12:569. 1838.
Acacia angulosa Bertol. Fl. Guat. 42. 1840.
Acacia insignis Mart. & Gal. in Bull. Acad. Brux. 10^2:315. 1843.
Acacia filicioides Trelease, Rept. Ark. Geol. Surv. 1888^4:178. 1891.
Acacia boliviana Rusby, in Bull. N. Y. Bot. Gard. 4:348. 1907.
Acaciella angustissima Britt. & Rose, in N. Am. Fl. 23:100. 1928.
Acaciella angulosa Britt. & Rose, loc. cit. 100. 1928.
Acaciella costaricensis Britt. & Rose, loc. cit. 101. 1928.
Acaciella Rensonii Britt. & Rose, loc. cit. 101. 1928.
?Acaciella Holtonii Britt. & Killip, in Ann. N. Y. Acad. Sci. 35:140. 1936.
Acaciella martensis Britt. & Killip, loc. cit. 1936.
Acaciella santanderensis Britt. & Killip, loc. cit. 1936.
Acacia Pittieriana Standl. in Field Mus. Publ. Bot. 18:489. 1937.

Bentham (Trans. Linn. Soc. 30:532. 1875) further lists the following species as synonyms of *A. angustissima: A. chlorantha* Zucc., *A. cuspidata* Schlecht., *A. elegans* Mart. & Gal., *A. elegans* Schlecht., *A. Hartwegi* Benth., *A. hirsuta* Schlecht., *A. hirta* Nutt., *A. penicillifera* Lag., *A. stipellata* Schlecht., *A. texensis* Torr., *A. umbellifera* Kunth.

Wiggins (Contr. Dudley Herb. 3:229–233. 1942) lists the following names as synonymous with several subspecies of *A. angustissima: Acacia Lemmonii* Rose, *A. hirta* var. *Shrevei* and var. *suffrutescens* Kearney & Peebles, *A. suffrutescens* Rose; *Acaciella breviracemosa* Britt. & Rose, *A. ciliata* Britt. & Rose, *A. hirta* Britt. & Rose, *A. Lemmonii* Britt. & Rose, *A. salvadorensis* Britt. & Rose, *A. Shrevei* Britt. & Rose, *A. Smithii* Britt. & Rose, *A. suffrutescens* Britt. & Rose.

Shrub or tree, the branchlets pubescent or puberulent to subglabrous, not noticeably lenticellate, longitudinally striate or angled. Leaves moderately large, bipinnate, the pinnae few to several pairs (about 15 pairs in Panamanian material cited), opposite or subopposite on the rachis, the leaflets numerous (up to 60 or more pairs per pinna); petiole up to a few cm. long, puberulent, eglandular, sulcate above; rachis up to 12 or more cm. long, like the petiole; pinnular rachis 3–9 cm. long, somewhat margined, seemingly eglandular, bearing basally a pair of stipule-like leaflets; leaflets nearly linear, usually about 6 mm. long and 1 mm. wide, acute (mostly bluntly so) apically, obliquely truncate basally, glabrous except ciliate-margined, dull above and below but darker above, the costa visible but secondary venation obscure; stipules linear-subulate, mostly 4–6 mm. long. Inflorescence a terminal or subterminal panicle of pedunculate umbels (heads),

Fig. 97. *Acacia angustissima*

these solitary to few-fasciculate from the (usually) defoliate nodes; peduncles usually about 1 cm. long; floral bracts obovate-spatulate, little more than 1 mm. long; pedicels mostly 1–2 mm. long, borne from the terminus of the peduncle in umbellate or very short-spicate fashion. Flowers few to several per umbel, whitish; calyx campanulate or turbinate, about 1 mm. long, glabrous or sometimes sparingly ciliate, the teeth short and broad; corolla funnelform, about 2 mm. long, glabrous, the lobes divided almost to the base; stamens many, about 4 mm. long, free except at the extreme base; anthers eglandular; ovary scarcely stipitate, glabrous or minutely puberulent, the style slightly exceeding the stamens. Legume linear-oblong, 4–8 cm. long and about 1 cm. wide, flat and thin, stipitate, glabrous in age; the seeds few, transverse.

Mexico to middle South America.

CHIRIQUÍ: R. Chiriquí Viejo, *P. White 35, 190.*

After examining Panamanian and Central American material of this species, and further noting its complicated synonymy, I must agree with Standley and Steyermark (Fieldiana: Bot. 24[5]:5. 1946) that a not-unusually-variable species has been made difficult by extreme splitting. Exact specific delimitation must await

the monographer, but again I concur with Standley and Steyermark's findings for Guatemala, in that Panamanian material won't "work" in Wiggins' separation of *A. angustissima* from *A. filicioides*.

2. ACACIA VILLOSA (Sw.) Willd. Sp. Pl. 4:1067. 1806.

Mimosa villosa Sw. Fl. Ind. Occ. 2:982. 1800.
Acacia lophanthoides DC. Prodr. 2:457. 1825.
Acacia carbonaria Schlecht. in Linnaea 12:571. 1838, fide Benth.
Acacia Cumingii Benth. in Hook. Lond. Jour. Bot. 1:525. 1842, fide Benth.
Acacia Valenzuelana A. Rich. Ess. Fl. Cub. 1:462. 1845.
Acaciella villosa Britt. & Rose, in N. Am. Fl. 23:104. 1928.
Acaciella Cumingii Britt. & Rose, loc. cit. 1928.
?Acaciella Oerstedii Britt. & Rose, loc. cit. ex char. 1928.

Shrub up to a few m. tall, unarmed, the branchlets heavily pubescent to almost glabrous. Leaves moderately large, bipinnate, the pinnae 4–10 pairs opposite on the rachis, the leaflets 9–25 pairs per pinna; petiole mostly about 2 cm. long, pubescent, normally eglandular, sulcate above; rachis similar to the petiole, 2–8 cm. long; pinnular rachis about 4 cm. long, pubescent, usually eglandular; leaflets broadly oblong or ovate, mostly about 8 or 9 mm. long, more or less inequilaterally obtuse apically, obliquely rounded basally, subglabrous or lightly pubescent above, appressed-pilose below, obscurely pinnately veined; stipules linear-lanceolate, 2–3 mm. long. Inflorescence of axillary, pedunculate heads, usually appearing more or less paniculate towards the tips of twigs because of insertion of peduncles at defoliate or immaturely foliate nodes; peduncles about 2 cm. long, pubescent; head compact, subglobose or very short-spicate, about 30-flowered. Flowers small, briefly pedicellate; calyx broadly cupulate, about 1 mm. long, shallowly 5-toothed, glabrous, sometimes ciliate; corolla funnelform-campanulate, 2–3 mm. long, glabrous except sometimes pubescent apically, deeply 5-parted; stamens numerous, about 5 mm. long. Legume oblong, 5–6 cm. long and almost 1 cm. wide, flat and thin, tapered basally, stipitate, lightly pubescent, the seeds transverse.

Southern Central America and West Indies.

According to Britton and Rose, this species is confined to Jamaica, while *A. Cumingii* is recognized as a distinct species known only from the Panamanian type. We have been unable to examine type material of either of these species, or, for that matter, of most of the synonyms listed. However, Bentham, author of *A. Cumingii*, with the accumulation of more material, later reduced his species to synonymy with *A. villosa* (Trans. Linn. Soc. 30:532. 1875). There seems to be no reason for not accepting Bentham's judgment, at least without reference to type material. Bentham's type sheet of *A. Cumingii (Cuming 1242)* thus becomes the record on which we base inclusion of *A. villosa* in Panama. No additional collections from there have come to our attention. Necessarily, the description above given is a composite from several sources and does not reflect any given specimen.

Acacia villosa somewhat resembles *A. angustissima*, but can be distinguished from it in having significantly broader and usually larger, more pubescent leaflets.

3. ACACIA HAYESII Benth. in Trans. Linn. Soc. 30:524. 1875.

Senegalia Hayesii Britt. & Rose, in N. Am. Fl. 23:114. 1928.
Senegalia acanthophylla Britt. & Rose, loc. cit. 117. 1928.
Acacia telensis Standl. in Field Mus. Publ. Bot. 4:308. 1929.
Acacia acanthophylla Standl. loc. cit. 18:488. 1937.

Liana or scandent shrub, armed with small, scattered, recurved thorns, the branchlets puberulent when young becoming glabrous. Leaves large, bipinnate, the pinnae usually about 10 pairs opposite on the rachis, the leaflets nearly 20 pairs per pinna; petiole 2 or more cm. long, puberulent above, bearing 1 or 2 cupulate, sessile glands; rachis up to 20 or more cm. long, similar to the petiole, bearing cupulate glands just below insertion of all or most pairs of pinnae; pinnular rachis 4–5 cm. long, presumably puberulent and with occasional small glands at the distal rachial nodes; leaflets linear-oblong, 8–10 mm. long, somewhat falcate, briefly mucronate apically, obliquely subtruncate basally, reportedly glabrous in a fragment of the type but appressed-pubescent below, the costa markedly excentric; stipules obovate? Inflorescence of 1 to few pedunculate spikes from subterminal, defoliate or minutely foliate nodes, thus appearing paniculate early; peduncles 1–2 cm. long, puberulent; spikes 10–12 mm. long, dense. Flowers subsessile, presumably whitish; calyx cupulate, about 2 mm. long and equally as broad, glabrous, moderately lobed; corolla cylindric-campanulate, about 4 mm. long, glabrous, rather briefly lobed; stamens many, 7–8 mm. long. Legume linear-oblong, flat, thin, stipitate, glabrous.

Panama, Costa Rica, Honduras.

CANAL ZONE: Mammee railroad station, *S. Hayes s. n.*

Examination of a photograph and a fragment of the type shows that specimens referable to the Honduran *A. telensis* and the Costa Rican *Senegalia acanthophylla* constitute a second record for *A. Hayesii,* previously known only from Panama.

4. ACACIA GLOMEROSA Benth. in Hook. Lond. Jour. Bot. 1:521. 1842.

Senegalia glomerosa Britt. & Rose, in N. Am. Fl. 23:116. 1928.

Usually a moderate to large tree, often buttressed, unarmed or sparingly armed with a scattering of recurved prickles on twigs and rachis, the branchlets pubescent when young becoming glabrous with age. Leaves quite large, bipinnate, the pinnae several to many pairs, the leaflets many (about 30) pairs per pinna; petiole 2–4 cm. long, tomentulose to subglabrous, flattened or sulcate above, bearing 1 (–2?) sessile gland usually below the middle; rachis up to 20 cm. long, similar to the petiole, sometimes aculeate below, usually bearing sessile glands above just below the distal few rachial nodes; pinnular rachis up to 10 cm. long, pubescent, glandular at the distal foliolar nodes; leaflets narrowly oblong or linear-oblong, mostly about 10 mm. long and 2–3 mm. wide, asymmetrically obtuse or acutish apically and thus subfalcate, obliquely truncate basally, puberulent or subglabrous above, appressed-pubescent below, the costa markedly excentric but not marginal, other

venation visible but obscure; stipules linear, caducous. Inflorescence a terminal panicle of pedunculate heads; peduncles 5–15 mm. long, tomentulose; heads compact, globose, 12- to 20-flowered, the bracts minute. Flowers small, cream or white; calyx cupulate, about 1 mm. long, puberulent; corolla funnelform, 2–3 mm. long, pubescent, the lobes about ⅓ as long as the tube; stamens many, mostly 5–6 mm. long. Legume linear-oblong, up to 20 cm. long and 3 cm. wide, rounded-subcuneate apically and basally, flat, puberulent becoming subglabrous in age, the margins slightly elevated, the seeds few, transverse.

Mexico to middle South America.

CANAL ZONE: Barro Colorado Island, *Aviles 10b.*

This species is quite variable, and in its extended range exhibits a number of diverse forms. Apparently it is commonly found as an erect tree, but sometimes it assumes somewhat the aspect of a liana. Most specimens are unarmed, but not a few bear scattered, recurved prickles, nor is this characteristic always associated with the subscandent habit. The Panamanian specimen cited possesses a longer pubescence than is typical for the species either in South America or north of Panama. It is also "atypical" in being armed and having more than the usual number of pinnae. Yet it can probably be considered within the specific boundaries of *A. glomerosa* despite uncertainties and perhaps intermediacy towards *A. tenuifolia.* The plant is evidently uncommon in Panama.

Our specimen (and others passing as the species) could almost as well be called *A. polyphylla* DC. as *A. glomerosa.* In fact, considered over their entire range, it is doubtful that *A. glomerosa* can be maintained as a species distinct from the older *A. polyphylla.*

5. ACACIA TENUIFOLIA (L.) Willd. Sp. Pl. 4:1091. 1806.

Mimosa tenuifolia L. Sp. Pl. 523. 1753.
Acacia paniculata Willd. Sp. Pl. 4:1074. 1806.
Mimosa grandisiliqua Vell. Fl. Flum. Ic. 11:*t. 37*. 1827, fide Benth.
Acacia grandisiliqua Benth. in Hook. Lond. Jour. Bot. 1:518. 1842.
Acacia Clausseni Benth., loc. cit. 1842, fide Benth.
Acacia martinicensis Presl, Bot. Bemerk. 65. 1844, fide Britt. & Rose.
Acacia microcephala A. Rich. Ess. Fl. Cub. 1:469. 1845, fide Britt. & Rose.
Senegalia tenuifolia Britt. & Rose, in N. Am. Fl. 23:118. 1928.

Tall liana, climbing through tops of trees, the branchlets puberulent or minutely tomentose, armed with broad-based, recurved thorns. Leaves large, bipinnate, the pinnae 20 or more pairs opposite on the rachis, leaflets numerous (about 70 pairs); petiole up to a few cm. long, terete, lightly tomentulose or puberulent, armed, bearing about 1 cm. from the base a sessile, longitudinally oblong gland; rachis about 20 cm. long, flattened or subsulcate and puberulent or tomentose above, armed with thorns, bearing at the uppermost several rachial nodes prominent orbicular glands; pinnular rachis about 7 cm. long, glabrous below, tomentose above, eglandular; leaflets asymmetrically linear, about 4 mm. long and less than 1 mm. wide, broadly and inequilaterally acute apically, obliquely truncate basally,

glabrous except ciliate-margined, the costa excentric, secondary veins prominent below but not above, dull; stipules caducous. Inflorescence paniculate, up to 3 or more dm. long, the primary axis armed, tomentulose; ultimate divisions of 1 to few pedunculate heads from nodes on which leaves have not yet developed; peduncles mostly 10–15 mm. long, tomentulose; heads several-flowered, globose, the floral bracts minute. Flowers dense, white; calyx funnelform-cupulate, about 1 mm. long, puberulent; corolla funnelform, scarcely 2 mm. long, minutely puberulent, deeply lobed; stamens many, 3–4 mm. long, glabrous, free except at the extreme base; anthers mostly eglandular (some apparently abortively glandular in bud); ovary pubescent, long-stipitate. Legume presumably linear-oblong, flat, thin, non-septate, glabrous in age.

Mexico to middle South America; West Indies.

DARIÉN: R. Chico, *Allen 4646;* El Real, *Allen 961.* SAN BLAS: Puerto Obaldía, *Pittier 4326.*

Britton and Rose (N. Am. Fl. 23) and various other authors have not recognized the synonymy of the South American *A. paniculata* and several Central American and Mexican "species" which probably represent the Linnean name *A. tenuifolia.* Yet a comparison of a series of Mexican, Central American, and West Indian specimens with South American material shows remarkably little difference. I have thus accepted Bentham's judgment that *A. paniculata* and *A. tenuifolia* are the same, and constitute merely one, not overly variable, species.

6. ACACIA RIPARIA HBK. Nov. Gen. & Sp. 6:276. 1824.

?Mimosa retusa Jacq. Enum. Pl. Carib. 34. 1762, fide Ind. Kew.
Mimosa paniculata West, Bidr. til Beskr. Ste.-Croix, 312. 1793; non authors, fide Ind. Kew.
Acacia Westiana DC. Prodr. 2:464. 1825, fide Benth.
Acacia guadalupensis DC. loc. cit. 1825.
?Mimosa plana Vell. Fl. Flum. Ic. 11:*t. 28.* 1827, fide Benth.
Acacia quadriglandulosa Mart. in Flora 20, Beibl. 2:110. 1838, fide Ind. Kew.
Acacia tubulifera Benth. in Hook. Lond. Jour. Bot. 1:520. 1842, fide Macbride.
Acacia sarmentosa Griseb. Fl. Brit. W. Ind. 221. 1861; non Desf., fide Ind. Kew.
Senegalia riparia Britt. & Rose, in Ann. N. Y. Acad. Sci. 35:144. 1936.

Shrub or tree (or often subscandent), sparingly aculeate on leaf rachis and twigs, with small, scattered, recurved thorns, the branchlets puberulent soon becoming glabrous, striate. Leaves moderately large, bipinnate, the pinnae 6–20 pairs opposite on the rachis, the leaflets many (mostly 20–40) pairs per pinna; petiole about 2 cm. long, sulcate above, subglabrous, bearing on the upper side 1 or more (usually 2) sessile, patelliform, longitudinally oblong glands; rachis up to 15 cm. long, sulcate and puberulent above, bearing glands like those of the petiole just below the several distal rachial nodes; pinnae usually 4–5 cm. long, eglandular; leaflets linear-oblong, 3–7 (usually 4–5) mm. long and about 1 mm. wide, more or less rounded to broadly acute apically, obliquely rounded or subtruncate basally, glabrous above and below, usually ciliate marginally and barbate at the base on the inner margin below, the costa subcentral except at the inequilateral base, it and a

few remote lateral veins prominent below, dull; stipules caducous or lacking. Inflorescence seemingly a raceme or panicle of pedunculate heads, these 1- to few-fasciculate from subterminal defoliate or tardily foliate nodes (nodes foliate in age or with fruit); peduncle 1–2 cm. long at anthesis, tomentulose; head dense, subglobose, about 30-flowered. Flowers sessile, whitish; calyx cupular, 1 mm. long, puberulent; corolla funnelform, 3–4 mm. long, puberulent apically, the lobes brief; stamens many, free, about 6 mm. long. Legume linear-oblong, usually 10–15 cm. long and 20–25 mm. wide, stipitate, tomentulose, usually sharp-beaked apically, flat and thin, the margins slightly elevated, the seeds transverse.

Middle South America to southern Central America; perhaps northern Central America and southern Mexico?

CANAL ZONE: Barro Colorado Island, *Aviles 14; Brown 148; Shattuck 436; Wetmore & Abbe 205; Woodworth & Vestal 512.* CHIRIQUÍ: San Felix, *Pittier 5141.*

Possibly the name *Acacia retusa* should apply to this species, but inasmuch as none of the types are available and Bentham himself had only "ex char." acquaintanceship with *Mimosa retusa* Jacq., which he listed as synonymous, we do not suggest any change in the familiar name, *A. riparia.* The species seems to grade into what commonly passes for *A. riparioides* in northern Central America and Mexico, differing from it primarily in having a somewhat longer corolla. The Chiriquí specimen is somewhat atypical, having larger flowers approaching those of *A. Hayesii.*

7. ACACIA FARNESIANA (L.) Willd. Sp. Pl. 4:1083. 1806.

Mimosa farnesiana L. Sp. Pl. 521. 1753.
Acacia acicularis Willd. Enum. 1056. 1809.
Vachellia farnesiana Wight & Arn. Prodr. Fl. Penins. Ind. Or. 272. 1834.
Listed by Bentham (Trans. Linn. Soc. 30:502. 1875) as additional synonyms are: *Acacia edulis* H. & B., *A. lenticellata* F. Muell., *A. leptophylla* DC., *A. pedunculata* Willd., *Farnesia odora* Gaspar., *Mimosa pedunculata* Poir., *M. scorpioides* Forsk.

Shrubs or occasionally small trees, the branchlets frequently somewhat pilose when young becoming glabrous, prominently lenticellate, armed with slender, solid (but having a soft pith), whitish, stipular spines up to about 3 cm. long, these not ant-infested. Leaves moderately small, bipinnate, the pinnae 2–6 pairs opposite on the rachis, the leaflets mostly 10–20 pairs per pinna; petiole up to 1 cm. long, terete except somewhat flattened above, usually tomentulose-subhirsute, bearing a sessile, oblong gland above the middle; rachis 1–5 cm. long, similar to the petiole, usually bearing a gland at insertion of the terminal pair of pinnae; pinnular rachis 1–3 cm. long, flattened above, often bearing a minute gland just below insertion of the terminal pair of leaflets; leaflets narrowly oblong, about 4 mm. long and 1 mm. wide, rounded apically, obliquely rounded or truncate basally, glabrous except frequently ciliate marginally, the costa prominent but other venation usually obscure. Inflorescence of axillary, pedunculate heads, these 1 to few from foliate nodes; peduncles mostly 1–2.5 cm. long, pubescent; heads dense,

globular; floral bracts narrowly oblanceolate, tipped white-pilose. Flowers small, yellow, sessile, fragrant; calyx funnelform-cupulate, about 1 mm. long, glabrous except on the shallow teeth; corolla narrowly funnelform, about 2 mm. long, glabrous except on tips of the lobes, the lobes relatively short; stamens many, little more than 3 mm. long, free except at the extreme base. Legume linear-oblongoid, up to 6 or 7 cm. long and almost 1 cm. wide, turgid-subterete, glabrous, longitudinally confluent-striate, tardily dehiscent, coriaceous, with a sweet pulp, pithy in age, septate, the seeds transverse.

Southern United States and Mexico to Argentina; West Indies; introduced into many parts of the Old World.

CANAL ZONE: Balboa, *Standley 30841;* Las Cruces Trail, *Hunter & Allen 682; Pittier 2621.* COCLÉ: Penonomé, *Williams 136.* PANAMÁ: R. Jagua, *Hunter & Allen 479;* Juan Díaz, *Standley 30535;* Nuevo San Francisco, *Standley 30703.*

This abundant species is of some economic importance. Leaves and pods serve as food for stock, while the heavy wood is used for fuel. The bark and legume are a source of tannin. An exudate from the trunk is reported useful as a mucilage. In southern France especially the species has been extensively cultivated for the perfume industry.

Acacia farnesiana is not clearly distinct from what commonly passes as another Linnean species in Central and northern South America, *A. tortuosa.* Without access to authentic material of these two species, no attempt is made to pass judgment on them. The pod of *A. tortuosa* is typically pubescent, while that of *A. farnesiana* is glabrous and shorter. Yet intermediacy in this character is found, as well as in other characteristics which are quite different in their extremes. The unsnarling of these few related species will require more critical study than is possible in this Flora.

8. ACACIA MACRACANTHA Humb. & Bonpl. ex Willd. Sp. Pl. 4:1080. 1806.

Acacia macracanthoides Bert. in DC. Prodr. 2:463. 1825.
Poponax macracanthoides Britt. & Rose, in N. Am. Fl. 23:89. 1928.
For multitudinous additional synonyms see Benth. Trans. Linn. Soc. 30:500. 1875.

Small tree, the branchlets armed with small to large, solid, paired stipular spines, in youth pubescent to subglabrous, later subglabrous and prominently lenticellate. Leaves moderately large, bipinnate, the pinnae 8– (reportedly) 60 pairs opposite on the rachis, the leaflets many. Petiole about 1 cm. long, pubescent, canaliculate above, bearing a longitudinally extended, crateriform gland slightly above the middle; rachis similar, gland-bearing only at terminal 1 to few rachial nodes; pinnae 2–3 cm. long, eglandular; leaflets linear or linear-oblong, mostly about 3 mm. long and scarcely 1 mm. wide, rounded or obtuse apically, obliquely rounded to subtruncate basally, glabrous or lightly pubescent, only the costa prominent; stipules modified as spines. Inflorescence of axillary, pedunculate heads, solitary or few-fasciculate; peduncles about 1 cm. long, tomentose, ebracteate (except at head); head orbicular, dense, less than 1 cm. in diameter; floral bracts linear-

spatulate, about 1 mm. long. Flowers small; calyx funnelform, about 1 mm. long, tomentulose apically; corolla tubular-funnelform, about 2 mm. long, glabrous except on the prominent lobes; stamens many, free, about 3 mm. long. Legume variable, linear, reported up to 10 cm. long and 12 mm. wide, subterete, straight or somewhat curved, usually puberulent and glandular.

Northern South America and West Indies; in a broad sense, possibly also northern Central America.

CANAL ZONE: Summit, *Lindsay 249* (presumably cultivated: at Canal Zone Experiment Gardens).

This very variable species is evidently not known in the wild from Panama, but occurs in Colombia and other portions of northern South America and the West Indies. It somewhat resembles *A. farnesiana*, these two species alone (in Panama) possessing solid stipular spines. *A. macracantha* is readily distinguished from *A. farnesiana* by the larger, multi-pinnular leaves.

9. ACACIA COOKII Safford, in Science n. s. 31:677. 1910.

Acacia bucerophera B. L. Robins., in Proc. Am. Acad. 49:502. 1913.
Myrmecodendron Cookii Britt. & Rose, in N. Am. Fl. 23:93. 1928.

Shrub or tree, the branchlets puberulent soon becoming glabrous and heavily lenticellate, armed with paired stipular spines, many of these becoming very large, blackish, hollow, ant-infested. Leaves large, bipinnate, the pinnae about 15 pairs, the leaflets about 30 pairs per pinna; petiole short, puberulent at least above, eglandular, sulcate above; rachis 8–15 cm. long, similar to the petiole, bearing cupulate glands just below insertion of all or most pairs of pinnae; pinnular rachis about 3 cm. long, tomentulose, eglandular; leaflets essentially linear, in the Panamanian specimen 3–4 mm. long and less than 1 mm. wide (usually about 6 mm. long for the species), asymmetric and bluntly acute apically, obliquely truncate basally, glabrous except ciliate-margined, the venation obscure; stipules modified as spines, these when enlarged (ant-infested) briefly connate at the base and resembling bull horns. Inflorescence of axillary pedunculate heads; peduncles short, clustered, bearing a 3-parted involucre near the middle; head very compact, globose. Flowers small, yellowish; calyx cupular, about 1 mm. long, glabrous; corolla funnelform, barely exceeding the calyx, glabrous except puberulent on tips of the lobes; stamens numerous, about 2 mm. long. Legume reported linear, 10–30 cm. long, somewhat compressed, usually curved, subglabrous, sessile, beaked apically, 2-valvate.

Guatemala, British Honduras, Honduras; on basis of cited specimen, Panama.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 462*.

The Panama specimen cited is very poor, and its determination cannot be entirely certain. It appears to match (descriptions and specimens of) *A. Cookii* better than *A. melanoceras*, the only other described species it might likely be. Our description is of the Panama plant insofar as possible (vegetative characters). The species is a member of the distinctive "bull-horn" group of Acacias.

10. ACACIA MELANOCERAS Beurl. in Sv. Vet. Akad. Handl. 1854:123. 1856.

Acacia multiglandulosa Schenck, in Fedde Rep. Sp. Nov. 12:362. 1913, fide Britt. & Rose.
Myrmecodendron melanoceras Britt. & Rose, in N. Am. Fl. 23:93. 1928.

Shrub or sometimes small tree, the branchlets puberulent when young, armed with large, terete, hollow, myrmecophilous, stipular spines, these briefly connate at the base and resembling bull horns. Leaves large, bipinnate, the pinnae normally at least 15 pairs, the leaflets 15–30 pairs per pinna; petiole 1–2 cm. long, sulcate above, usually puberulent, bearing on the upper side a number of conic glands in one or more rows; rachis similar, as much as 4 dm. long, bearing a conic gland just below insertion of most pairs of pinnae; pinnular rachis mostly 4–5 cm. long, if glandular obscurely so; leaflets linear, about 5–6 mm. long and scarcely more than 1 mm. wide, inequilaterally obtuse apically, obliquely rounded basally, glabrous, dull, with a single prominent vein; stipules modified as large, lustrous, brown or black spines as much as 4 or 5 cm. long. Inflorescence a terminal, raceme-like grouping of pedunculate heads, these 1 to few from the axils of defoliate or minutely foliate nodes; peduncles short, 2–12 mm. long, bearing near the base a 3- to 4-partite involucre; heads globular, densely flowered, the floral bracts peltate, about equalling the flowers. Flowers minute, yellow; calyx cupular, about 1 mm. long, glabrous or puberulent apically, obscurely lobed; corolla funnelform, little more than 1 mm. long, puberulent apically, more prominently lobed; stamens many, 2–3 mm long. Legume linear-oblong, up to 10 cm. long, slightly compressed-subterete, short-beaked, longitudinally striate, glabrous, tardily dehiscent.

Panama.

CANAL ZONE: Barro Colorado Island, *Aviles 20b; Kenoyer 373;* France Field, *Fairchild Aug. 1924; Shropshire, Feb. 1945.*

The species is known only from Panama (types = *Billberg 289, 1825,* from Portobello, Colón). Possibly one or two species of northern Central America, such as *A. Donnelliana, A. Cookii* and *A. globulifera,* may prove to be the same entity; but insufficient collections are available to pass judgment on this question.

11. ACACIA COSTARICENSIS Schenck, in Fedde Rep. Sp. Nov. 12:361. 1913.

Acacia panamensis Schenck, loc. cit. 362. 1913, fide Britt. & Rose.
Acacia penonomensis Safford, in Jour. Wash. Acad. 4:363. 1914, fide Britt. & Rose.
Acacia Nelsonii Safford, loc. cit. 1914, fide Britt. & Rose.
Myrmecodendron costaricense Britt. & Rose, in N. Am. Fl. 23:93. 1928.

Shrub or small tree, the branchlets glabrous and laxly lenticellate, armed with large, hollow, myrmecophilous stipular spines shaped like the horns of a bull. Leaves large, bipinnate, the pinnae 4–12 pairs opposite on the rachis, the leaflets 13–24 pairs; petiole almost 2 cm. long, glabrous, flattened or sulcate above, bearing on the upper side below the middle usually 2–3 conic glands; rachis up to 15 cm. long, similar to the petiole, usually eglandular; pinnae somewhat lax, glabrous, eglandular, the axis margined; leaflets linear, usually 8–9 mm. long and only slightly more than 1 mm. wide, inequilaterally rounded or obtuse apically, obliquely

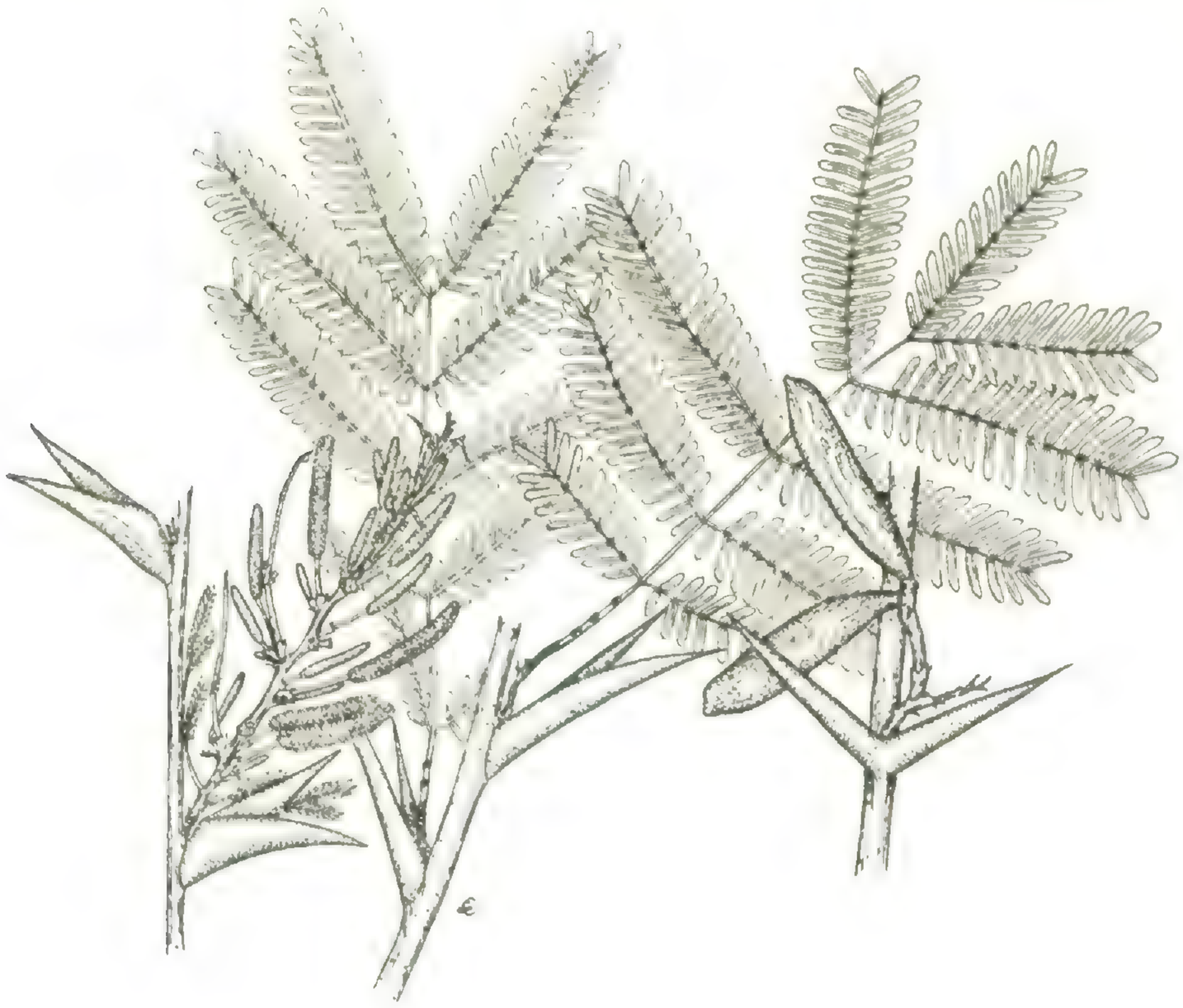

Fig. 98. *Acacia costaricensis*

rounded basally, glabrous and dull above and below, with 2–3 prominent palmate veins from the base; stipules large, terete spines frequently 3–4 cm. long, those of a pair fused at the base, lustrous, brownish. Inflorescence of condensed, peduncu-late, axillary spikes about 3 or 4 cm. long; peduncle usually about 1 cm. long, bearing a tripartite involucre near the base; floriferous portion elongate, ament-like, becoming thicker in fruit; bractlets peltate, equalling the flowers. Flowers minute, very dense on the spike, yellowish; calyx cupulate, less than 1 mm. long, glabrous (or minutely puberulent marginally), obscurely lobed; corolla funnel-form, little more than 1 mm. long; stamens many, about 2 mm. long. Legume narrowly oblong, mostly 4–5 cm. long, bluntly and briefly beaked apically, sessile, slightly compressed-subterete, glabrous but more or less scurfy, longitudinally striate, pulpy, reportedly 2-valvate but apparently tardily dehiscent, the seeds obliquely longitudinal.

Mexico to Colombia.

CANAL ZONE: Chivi-Chivi trail, *Maxon & Harvey 6579;* Miraflores, *Allen 1743.* CHIRIQUÍ: Puerto Remedios, *Pittier 3378.* COCLÉ: Penonomé, *Williams 113* (photo). PANAMÁ: R. Abajo, *Bro. Paul 267;* Bella Vista, *Pittier 6785; Standley 25374; Macbride 2758;* Nuevo San Francisco, *Standley 30737.*

This species, a member of the interesting "bull-horn" group very prominent in northern Central America and Mexico, runs into *A. Collinsii* (= *A. yucatanensis*) and possibly *A. hirtipes* and *A. Hindsii* of that region. Three or four species of

Acacia in Panama have the large, hollow, ant-infested stipular thorns the basis for such popular names as "cockspur," *casa de hormigas, cornizuelo,* etc. Of these *A. costaricensis* can be readily distinguished by the spicate inflorescence.

12. ACACIA SPADICIGERA Schlecht. & Cham. in Linnaea 5:594. 1830.

Acacia nicoyensis Schenck, in Fedde Rep. Sp. Nov. 12:360. 1913.
Acacia cubensis Schenck, loc. cit. 1913, fide Britt. & Rose.
Acacia furcella Safford, in Jour. Wash. Acad. 4:359. 1914, fide Britt. & Rose.
Acacia Hernandezii Safford, loc. cit. 358. 1914, fide Britt. & Rose.
Tauroceras spadicigerum Britt. & Rose, in N. Am. Fl. 23:85. 1928.

Shrub or small tree, the branchlets glabrous, armed with large, hollow, grayish, paired, myrmecophilous stipular spines connate at the base and resembling bull horns. Leaves moderate, bipinnate, the pinnae mostly 2–8 pairs, the leaflets many (12–30 or more) pairs per pinna; petiole about 1 cm. long, glabrous, expanded above into a large, longitudinally oblong, glandular area bearing a solitary, extended conic "nectary"; rachis a few cm. long, glabrous, sulcate above, sometimes bearing an orbicular gland at insertion of the lowermost pair of pinnae; pinnae up to 7 cm. long, glabrous; leaflets linear, 5–10 mm. long and almost 2 mm. wide, rounded-mucronulate apically, obliquely truncate basally, glabrous, both costa and secondary veins noticeable; stipules modified as large, myrmecophilous spines as much as 8 cm. long. Inflorescence of axillary, pedunculate spikes; peduncles very short, usually about 3 mm. long, glabrous, bearing below the middle a 4-partite involucre; spikes oblong, mostly about 3 cm. long and almost 1 cm. wide, gross, spadix-like, the tips of the bractlets protruding. Flowers very small, very condensed, presumably yellow; calyx tubular-truncate, about 1 mm. long, glabrous; corolla included within calyx; stamens scarcely 2 mm. long. Legume oblong, about 8 cm. long (including beak) and about 13 mm. in diam., stipitate, long-beaked (the beak about 3 cm. long), terete, indehiscent, pulpy, the pericarp thin, the seeds transverse.

Mexico, northern Central America, Costa Rica; Panama?

This species is reported by modern authors from Costa Rica but not from Panama. Bentham incorrectly listed *Cuming 1270* from Panama as *A. spadicigera* (Trans. Linn. Soc. 30:514), the specimen actually being *A. costaricensis*. Nevertheless, there remains a distinct possibility that the species does occur and will eventually be collected in Panama. As with a number of pulpy legumes, the fruit of this species is commonly eaten by local peoples in Central America.

SPECIES DOUBTFULLY RECORDED FROM PANAMA

Acacia Hindsii Benth. (Hook. Lond. Jour. Bot. 1:504. 1842) has been reported from Panama, apparently in error. A specimen so determined in the herbarium of the Chicago Museum of Natural History proved to be *A. costaricensis*, and no additional collections from Panama of *A. Hindsii* have come to my attention in

any of the larger United States herbaria. This species is characterized by having the legume reputedly dehiscent only along the lower suture, being the only species among the "bull-horn" Acacias having this characteristic.

7. MIMOSA L.

Mimosa L. Sp. Pl. 516. 1753.

?Panthocarpa Raf. Neogen. 2. 1825, fide Dalla Torre & Harms.
Eburnax Raf. New Fl. N. Amer. 1:42. 1836, in part.
Lomoplis Raf. Sylva Tell. 118. 1838.
Sensitiva Raf. loc. cit. 119. 1838.
Pteromimosa Britt., in N. Am. Fl. 23:171. 1928.
Neomimosa Britt. & Rose, loc. cit. 172. 1928.
Mimosopsis Britt. & Rose, loc. cit. 174. 1928.
Acanthopteron Britt., loc. cit. 179. 1928.
Haitimimosa Britt., loc. cit. 179. 1928.

Coarse herbs or shrubs (in Panama), usually sprawling, decumbent to subscandent, heavily or lightly armed (in all Panamanian species except sometimes *M. pusilla*) with recurved thorns, variously pubescent. Leaves often sensitive (responding visibly to touch or other stimuli), bipinnate, the pinnae 1 to many pairs, opposite, the leaflets 2 to many pairs per pinna; petioles pulvinate, eglandular (in Panama), usually aculeate; rachis eglandular but often spinose- or subulate-appendaged; pinnae usually short, pulvinate, the pulvinus commonly setose; leaflets large and few or more commonly small and many, inequilateral basally, if pubescent usually strigose; stipules narrow, subpersistent. Inflorescence of pedunculate heads (in all Panamanian species) or spikes, these axillary from lower foliate and/or subterminal non-foliate nodes; floral bractlets usually shorter than the corolla, subpersistent. Flowers pinkish or whitish, normally sessile, small, numerous, usually perfect; calyx commonly very minute; corolla several times exceeding the calyx, usually funnelform, 3–6 (mostly 4) -lobed, the lobes equalling or shorter than the tube, valvate; stamens as many as or twice as many as the corolla lobes, free, exserted, the small anthers eglandular; ovary generally short, few- to many-ovulate, the style about equalling the stamens, the stigma not expanded. Legume linear to broadly oblong, flat, thin, with persistent margins, usually (as with all Panamanian species) transversely articulate, commonly setose-spinose.

Primarily western hemisphere from United States to Argentina, especially abundant in tropics and subtropics; a few species are known from Africa and Asia.

On the whole, the genus presents a rather natural grouping, grading, however, into certain (generally recognized) segregates such as *Schrankia*. Many of the species of *Mimosa* seem constantly distinctive, while others have evolved into a number of indistinct forms which are usually graced with (doubtfully tenable) specific names. As a result considerable condensation is in order, a common condition among most genera of the Mimosoideae.

In addition to Bentham's original classical work on the Leguminosae, B. L. Robinson presented a "Revision of the North American and Mexican species of

Mimosa" (Proc. Am. Acad. 33:305. 1898). Britton and Rose in the 'North American Flora' list about 150 species of *Mimosa* north of South America, of which 9 have been collected in Panama. A number of additional species are known from neighboring regions, some of which well may be collected in Panama eventually. Listed from Costa Rica are: *M. albida, M. Calderoni, M. dormiens, M. flavescens,* and *M. Watsonii.* Listed from Colombia by Britton and Killip (Ann. N. Y. Acad. Sci. 35:148–154. 1936) are: *M. albida, M. Andreana, M. colombiana, M. debilis, M. dormiens, M. esmeraldae, M. flavescens, M. floribunda, M. jiramenensis, M. Killipii, M. Lawranceana, M. leiocarpa, M. Martensis, M. oligacantha, M. polycarpa, M. quitensis, M. santanderensis, M. spiciflora, M. tenuiflora,* and *M. Trianae,* a number of them recognized species of long standing.

a. Pinnae a single pair per leaf.
  b. Leaflets 10–40 mm. long, 4–15 mm. wide, 2–6 pairs per pinna; legume 4–12 mm. wide.
    c. Leaflets only 2 pairs per pinna, mostly 3–4 cm. long.
      d. Leaflets 10–15 mm. wide, ovate to elliptic (broadest below the middle); legume mostly 6–10 mm. wide; head more robust.
        e. Twigs glabrous or nearly so, copiously armed; leaflets sparingly if at all strigose; floral bractlets prominent, exceeding and obscuring the subglabrous buds ..... 1. M. VELLOZIANA
        ee. Twigs usually pubescent, sparingly aculeate; leaflets densely strigose; floral bractlets no longer than and scarcely visible among the puberulent buds ..... 2. M. ALBIDA
      dd. Leaflets mostly 4–10 mm. wide, more or less obovate (broadest above the middle); legume about 4 mm. wide; head less robust.. 3. M. PANAMENSIS
    cc. Leaflets 3 or more pairs per pinna, mostly 1–3 cm. long ..... 4. M. CASTA
  bb. Leaflets 3–12 mm. long, 1–2 mm. wide, about 16 pairs per pinna; legume about 4 mm. wide ..... 5. M. PUDICA
aa. Pinnae 2 or more pairs per leaf, at least on some or most leaves.
  b. Rachis very condensed or obsolete, the pinnae thus subdigitate; stamens as many as the corolla lobes.
    c. Pinnae no more than 2 pairs; peduncle about 2 cm. long in maturity ..... 5. M. PUDICA
    cc. Pinnae 3–5 pairs; peduncles short, about 1 cm. long ..... 6. M. POLYDACTYLA
  bb. Rachis approximating or exceeding the petiole, the pinnae comparatively remote and quite obviously not subdigitate; stamens twice as many as the corolla lobes.
    c. Slender plants, with shorter thorns and softer pubescence; leaflets with 1 main vein or costa; pinnae usually 2–5 (1–8) pairs; rachis approximating the petiole, setiform-appendaged.
      d. Corolla membranous, not striate; pubescence not glandular; twigs strongly angled or terete.
        e. Twigs terete or nearly so, scarcely if at all aculeate; pinnae 1–3 pairs; secondary veins of leaflet conspicuous; heads somewhat obconic, conspicuously bracteate ..... 7. M. PUSILLA
        ee. Twigs strongly angled or tetragonal, heavily aculeate; pinnae usually 4–5 pairs; secondary veins of leaflet obscure; heads nearly orbicular, inconspicuously bracteate ..... 8. M. INVISA
      dd. Corolla striate; pubescence almost always glandular-tipped; twigs subterete ..... 9. M. SOMNIANS
    cc. Coarse plant, formidably armed and setose-hispid; leaflets longitudinally few-veined; pinnae usually at least 10 pairs; rachis much exceeding the petiole, spinose at insertion of the pinnae ..... 10. M. PIGRA

1. Mimosa Velloziana Mart. Herb. Fl. Bras. 185. 1837.

Mimosa viva Vell. Fl. Flum. Ic. 11:*t. 33*. 1827, not L.

Woody, vine-like shrub, scandent or decumbent, large or small, the branchlets subterete, glabrous or subglabrous, copiously armed with recurved thorns. Leaves reportedly sensitive, moderate, bipinnate, the pinnae a single pair, the leaflets only 2 pairs per pinna; petiole up to 5 or 6 cm. long, subglabrous, eglandular, armed with recurved thorns, conspicuously pulvinate basally, apiculate terminally; pinnular axis 1–2 cm. long, appendaged above the pulvinus, scarcely if at all aculeate; leaflets asymmetrically ovate-lanceolate, mostly 3–4 cm. long and 10–15 mm. wide, the inner member of the lower pair very reduced, acute-subacuminate apically, obliquely rounded basally, glabrous and darker above, sparingly setose-strigose or subglabrous and lighter below, setose-ciliate on the margins; stipules ovate, about 3 mm. long, ciliate. Inflorescence of axillary, pedunculate heads, often few-fasciculate; peduncles mostly 1–2 cm. long, unarmed, subglabrous; heads ovoid, compact, multiflorate; floral bractlets linear-lanceolate or linear-oblanceolate, setose-fimbriate, about 2 mm. long. Flowers small, sessile, reportedly pinkish; calyx exceedingly minute, fimbriate-lobed; corolla funnelform, about 2 mm. long, subglabrous, the 4 lobes less than ½ the length of the tube; stamens 4, 7–8 mm. long, the anthers orbicular; ovary setose. Legume oblong, 1–3 cm. long and 8–10 mm. wide, flat, segmented, densely setose-spinose on the persistent margins but little if at all so on the segments, otherwise glabrous.

Southern Mexico through Central and South America to Paraguay.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 293*. CANAL ZONE: "Chagres", *Fendler 91*; "Panama", *Seemann 100*.

The species usually occurs in clearings, and fast becomes a pest, forming nearly impenetrable tangles which tear clothing and flesh. It is reported sensitive to touch, contracting the leaves when disturbed.

Mimosa Velloziana has consistently been regarded as a distinct and tenable species, in spite of the fact that it does not always exhibit hard and fast demarcation from certain species of greater antiquity. Remarkably like it, but usually without prominent, appressed, pectinate floral bractlets are *M. sensitiva* L. of Brazil (usually exhibiting markedly greater pubescence of twig, leaf and legume); *M. albida* H. & B. ex Willd. of the same general range (also more pubescent); *M. floribunda* Willd. = *M. strigosa* Willd. (which, according to Britton and Rose, are synonyms of *M. albida*); and five or six more recent species. Bentham states (Trans. Linn. Soc. 30:390. 1875): "[*M. sensitiva, M. Velloziana*] and the three or four following species [which include *M. albida*] pass so nearly one into the other that they would probably all have been included by Linnaeus under his *M. sensitiva*." Bentham likewise included *M. jiramenensis* Karst. of Colombia as but a variety of *M. Velloziana*, but Britton and Killip (Ann. N. Y. Acad. Sci. 35:150. 1936) recognize it as a distinct species.

2. MIMOSA ALBIDA Humb. & Bonpl. ex Willd. Sp. Pl. 4:1030. 1806.

Mimosa strigosa Willd. Sp. Pl. 4:1030. 1806, fide Britt. & Rose.
Mimosa floribunda Willd. loc. cit. 1031. 1806, not Vent., fide Britt. & Rose.
Mimosa Willdenowii Poir. in Lam. Encycl. Meth. Suppl. 1:50. 1810.
Mimosa racemosa Schlecht. in Linnaea 12:557. 1838, fide Britt. & Rose.
Mimosa albida var. *floribunda* B. L. Robins. in Proc. Am. Acad. 33:311. 1898, fide Britt. & Rose.
Mimosa albida var. *strigosa* B. L. Robins. loc. cit., fide Britt. & Rose.
Mimosa albida var. *euryphylla* B. L. Robins. loc. cit., fide Britt. & Rose.
Mimosa albida var. *glabrior* B. L. Robins. loc. cit., fide Britt. & Rose.
Mimosa Williamsii Standl. in Contr. U. S. Nat. Herb. 18:105. 1916, not Rusby.
Mimosa Standleyi Macbride, in Contr. Gray Herb. 59:12. 1919.

Usually a slender vine with trailing or clambering stems; branchlets terete, glabrous or more commonly (Panama) strigose or lightly tomentose, unarmed or

Fig. 99. *Mimosa albida*

sparingly aculeate (Panama). Leaves moderate, bipinnate, the pinnae a single pair, the leaflets only 2 pairs per pinna; petiole up to 5 or 6 cm. long, eglandular, pubescent like the branchlets, sometimes aculeate, apiculate terminally; pinnular axis 1–2 cm. long, appendaged above the pulvinus, usually pubescent; leaflets usually asymmetrically oblong or elliptic, broadly acute or obtuse and briefly mucronate apically, obliquely rounded basally, the costa strongly excentric, strigose-pubescent above and more heavily so below; stipules linear to linear-lanceolate, 3–4 mm. long, rigid, erect, pectinate-ciliate. Inflorescence of axillary, pedunculate heads, sometimes few-fasciculate; peduncles mostly 1–2 cm. long; heads ovoid, compact, multiflorate; floral bractlets sublinear, with subulate tips, scarcely equalling the corolla. Flowers small, sessile, whitish; calyx campanulate, minute; corolla funnelform, about 2 mm. long, usually 4-lobed, not striate, usually tomentulose apically in bud; stamens 4 (5?), mostly 4–6 mm. long, glabrous; ovary glabrous or subglabrous. Legume more or less oblong, 1–3 cm. long and usually 6–7 mm. wide, flat, 1- to few-segmented, short-stipitate or subsessile, acute and subulate apically, setose-strigose or setose-spinose marginally.

Mexico to northern South America.

COCLÉ: Penonomé, *Williams 101*.

The cited specimen is the type collection for M. *Williamsii* Standl. (= M. *Standleyi*). It appears to be another of the aberrant forms commonly found in M. *albida*, a species known to vary extravagantly. Standley himself, with the original description of M. *Williamsii*, stated his species to be closely related to M. *albida*. Bentham (Trans. Linn. Soc. 30:390. 1875) lists Panama as included in the range of M. *albida* as he interpreted the species. Without any attempt to evaluate B. L. Robinson's subdivision of M. *albida* into varieties, I have here followed the 'North American Flora' in pigeon-holing a number of different variants, including M. *Williamsii* Standley, under the early name of M. *albida*. Even then it is difficult to find any hard-and-fast difference between this species and M. *sensitiva* L. of South America.

M. *albida* is of a weedy nature, invading cleared and pastured lands where it often becomes a serious pest in forming nearly impenetrable tangles. Like other members of the group it is at least moderately "sensitive" to contact.

3. Mimosa panamensis (Benth.) Standl. in Contr. U. S. Nat. Herb. 18:104. 1916.

Mimosa debilis H. & B. ex Willd. var. *panamensis* Benth. in Trans. Linn. Soc. 30:391. 1875.

A sprawling subherbaceous or suffruticose annual, the branchlets slender, sparingly to heavily hirsute, sparingly to moderately recurved-aculeate. Leaves moderately small, bipinnate, the pinnae a single pair, the leaflets only 2 pairs per pinna; petiole slender, 15–40 mm. long, sparingly armed or unarmed, eglandular; pinnular axis very short, seldom 5 mm. long; leaflets asymmetrically obovate to oblong, usually broadest above the middle, up to 2 cm. long and 4–7 mm. wide, the inner

member of the basal pair very reduced, usually obtuse or rounded and briefly mucronate apically, obliquely rounded basally, strigose-pubescent on both upper and (more heavily) lower surface, the venation prominent below; stipules linear, about 4 mm. long, pectinate-ciliate. Inflorescence of axillary, pedunculate heads, racemose terminally because of non-foliate nodes; peduncles up to 3 cm. long, subglabrous; heads dense, globular; floral bractlets linear-lanceolate, 1–2 mm. long, pectinate-ciliate. Flowers small, sessile, pinkish-white?; calyx campanulate, minute; corolla funnelform, about 2 mm. long, membranous, usually puberulent apically, 4- (5?) -lobed, the lobes less than half as long as the tube; stamens 4 (5?), about 6 mm. long, glabrous, the anthers orbicular; ovary subglabrous. Legume oblong, mostly 1–1.5 cm. long and 3–5 mm. wide, flat, few-segmented, the persistent margins heavily setose-spinose, the valves less heavily so.

Costa Rica, Panama, and Colombia.

CANAL ZONE: Ancón Hill, *Bro. Celestine 66; Standley 25191, 26321; Killip 12082.* COCLÉ: Aguadulce, *Pittier 4952;* Nata, *Seemann 98.* PANAMÁ: Corozál Road, *Standley 26784, 29173; Killip 3146;* northeast of Panama City, *Bro. Paul 206.* VERAGUAS: Soná, *Allen 1061.*

It is possible that the species should be *M. sensitiva* L. (considered broadly) or but a form of *M. albida* (which in turn does not seem to be clearly distinct from *M. sensitiva*). The point is debatable as to whether it is worthy of better than varietal rank, but as a variety it would seem as much akin to *M. albida* or *M. Velloziana* as to *M. debilis.*

4. MIMOSA CASTA L. Sp. Pl. 518. 1753.

Mimosa dominiciana Desv. in Ann. Sci. Nat. Bot. 9:424. 1826, fide Benth.

Scandent, suffruticose plants, the branchlets subterete but angled or ridged, glabrous or somewhat pubescent, densely armed with recurved, broad-based thorns. Leaves moderately large, bipinnate, the pinnae 1 pair, the leaflets mostly 3–4 pairs; petiole elongate, as much as 10 cm. long, eglandular, callous basally, apiculate terminally, armed like the twigs; pinnae 3–7 cm. long, the rachis pulvinate and usually aculeate; leaflets inequilaterally elliptic to oblong-lanceolate, mostly 10–30 mm. long and 5–15 mm. wide, acute apically, obliquely rounded basally, callous basally and with a few conspicuous palmate veins, setose-ciliate on the margins, sometimes with a few appressed setae on the lower surface; stipules narrowly linear-lanceolate, falcate, commonly about 5 mm. long, striate. Inflorescence of axillary, pedunculate heads; peduncles short, 5–15 mm. long; heads globular, several- to many-flowered, the floral bractlets linear-lanceolate, 1–2 mm. long. Flowers small, sessile, dense, whitish; calyx very minute; corolla funnelform, 1–2 mm. long, glabrous, 4-lobed, the lobes half as long as the tube; stamens 4, about 1 cm. long, free, glabrous; ovary short, setose, bilateral, the style slightly exceeding the stamens. Legume oblong, usually 30–40 mm. long and about 12 mm. wide, flat, glabrous, 4- to 5-segmented, the margins setose-spinose and persistent.

Panama and north coast of South America to Brazil; Lesser Antilles.

CANAL ZONE: Miraflores, *Pittier 2198;* Pedro Miguel, *Allen 2.*

5. MIMOSA PUDICA L. Sp. Pl. 518. 1753.

Bentham (Trans. Linn. Soc. 30:397. 1875) lists the following synonyms for *M. pudica: M. endymionis* Mart.; *M. hirsuta* Moç. & Sess.; *M. hispidula* HBK.; *M. irritabilis* Presl; *M. pudibunda* Willd.; *M. striato-stipula* Steud.; *M. tetrandra* H. & B.; *M. unijuga* Duchass. & Walp.

Prostrate herb to somewhat suffruticose, the branchlets terete, glabrous or pubescent (often both glabrous and pubescent branchlets on same plant), heavily or lightly armed with recurved thorns, the thorns broad-based and black-tipped. Leaves moderately small, sensitive, bipinnate, the pinnae 1 or (more commonly) 2 pairs, the leaflets mostly about 16 pairs; petiole elongate, up to 4 cm. long, subterete, glabrous or pubescent and sometimes even aculeate, eglandular, with a conspicuous basal pulvinus; rachis short (2–3 mm.) or obsolete; pinnae congested, the pinnular rachis and pulvinus usually setose, with a pair of squami just above the pulvinus; leaflets linear or linear-oblong, 3–12 mm. long and mostly 1–2 mm. wide, abruptly acute or subobtuse apically, inequilaterally truncate or rounded basally, with 1 or 2 smaller basal veins in addition to the costa, venation remote but visible below, glabrous except the margins (and sometimes the lower surface) yellow-setose; stipules linear-lanceolate, falcate, 4–8 mm. long, setose. Inflorescence of axillary, pedunculate, head-like spikes; peduncle about 2 cm. long in maturity; spikes short, very condensed, many-flowered; floral bractlets linear-lanceolate or linear-oblanceolate, setose. Flowers pinkish, sessile; calyx extremely minute, only a fraction of a mm. long; corolla funnelform, 1–2 mm. long, glabrous, 4-lobed, the lobes about half as long as the tube; stamens 4, about 7 mm. long, free, glabrous; anthers minute, nearly orbicular; ovary small, glabrous, bilateral, the style about equalling the stamens. Legumes typically in a dense cluster, usually 10–15 mm. long and about 4 mm. wide, flat, glabrous, segmented, somewhat constricted between the articulated, 1-seeded segments, heavily setose-aculeate on the margins, the margins persisting after dispersal of the segments.

Southern Mexico to middle South America; West Indies. Introduced into Old World tropics; cultivated under glass in temperate regions.

BOCAS DEL TORO: Chiriquí Lagoon, *H. von Wedel 1492, 1619, 2870.* CANAL ZONE: "Chagres", *Fendler 96;* Gatún, *Hayes 159;* Las Cruces trail, *Hunter & Allen 726;* Quebrada La Palma, *Dodge & Allen 17358.* CHIRIQUÍ: Boquete, *Woodson & Schery 721;* Llanos del Volcán, *Seibert 324, 351.* COCLÉ: Aguadulce, *Pittier 4861;* Penonomé, *Williams 100.* PANAMÁ: Chepo, *Pittier 4760;* Taboga Island, *Standley 27052.*

This interesting "plant oddity" is well known for its ability to quickly fold and droop its leaves with contact or other stimuli. Walking through a field of "sensitive plant" in the tropics one can look back and easily discern the path taken because of the altered position of the leaves brushed against. The plant shows a similar response to darkness or disturbance by rainfall. It is frequently kept as a curiosity, both in the tropics and in greenhouses of temperate climates. The species is abundant in open lowland areas in Panama, but also occurs at higher

elevations. It is similar to *M. polydactyla,* and is distinguishable from the Mexican *M. affinis* only by a difference in legume setae.

6. MIMOSA POLYDACTYLA Humb. & Bonpl. ex Willd. Sp. Pl. 4:1033. 1806.

An herbaceous to suffruticose plant, the branchlets terete, pubescent or glabrate, sparingly or densely armed with broad-based, black-tipped thorns. Leaves moderate or moderately large, sensitive, bipinnate, the pinnae 3–5 (usually 4) pairs clustered at the apex of the petiole (hence subdigitate), the leaflets usually about 30 or more pairs; petiole elongate, up to 8 cm. long, eglandular, usually setose; rachis very condensed, scarcely 3 mm. long; pinnae as much as 12 cm. long, the basal pinnular pulvinus setose; leaflets linear, 4–9 mm. long and usually 1–2 mm. wide, usually acute apically, inequilaterally rounded basally, the costa and remote lateral veins subprominent, glabrous except setose marginally and occasionally below; stipules linear-lanceolate, falcate, about 5 mm. long, setose. Inflorescence of axillary, pedunculate heads or very short spikes; peduncles short, usually little more than 1 cm. long; heads dense, many-flowered; floral bractlets sublinear, setose-laciniate. Flowers pinkish or purplish, sessile; calyx extremely minute; corolla funnelform, about 2 mm. long, glabrous, 4-lobed; stamens 4, several mm. long, free; ovary glabrous, bilateral, the style equalling the stamens. Legumes typically in a dense cluster, usually 10–15 mm. long and about 4 mm. wide, flat, glabrous, segmented, somewhat constricted between the articulated, 1-seeded segments, heavily setose-aculeate on the margins, the margins persisting after dispersal of the segments.

Panama to Brazil.

"WESTERN PANAMÁ": *Stork,* July-Aug. 1923.

Mimosa polydactyla is apparently less frequent in its range than is *M. pudica.* It is very similar to *M. pudica,* but possesses more numerous pinnae and leaflets and has shorter peduncles than is characteristic of the latter species.

7. MIMOSA PUSILLA Benth. in Bot. Voy. Sulphur, 90. 1844.

Low, prostrate or semi-prostrate herb, the branchlets glabrous to setose or lightly hirsute, scarcely armed (thorns, if present, few, nearly straight, weak), terete or subterete, inconspicuously lenticellate. Leaves small, bipinnate, the pinnae 1–3 pairs opposite on the rachis, the leaflets 5–20 pairs per pinna; petiole less than 1 cm. long, glabrous or pubescent like the twigs, terete, eglandular; rachis similar to the petiole, eglandular but with setiform appendages, the rachial internodes about equalling the petiole; pinnae remote (i. e. not subdigitate), 5–35 mm. long; leaflets linear-oblong, 3–8 mm. long and 1–1.5 mm. wide, broadly acute to obtuse and briefly mucronulate apically, obliquely rounded or subtruncate basally, glabrous except often ciliate-margined, the costa and lateral veins quite conspicuous (the lateral veins curving upward to subparallel the costa); stipules ovate, 2–4 mm. long, acuminate, longitudinally striate. Inflorescence of solitary, axillary, pedunculate heads; peduncles short, rarely even as much as 1 cm. long, pubescent as the

twigs, ebracteate except at the head; head small, more or less obconic, few- to several-flowered, nearly ensheathed (at least in youth) by the prominent floral bracts; floral bracts ovate-lanceolate, usually 2–3 mm. long, subscarious and striate, usually ciliate but otherwise glabrous. Flowers small, pinkish; calyx campanulate, minute, glabrous; corolla funnelform, 1–2 mm. long, membranous, glabrous, 4-lobed; stamens 8 (sometimes fewer?), 3–4 mm. long, glabrous; ovary glabrous. Legume oblong, typically less than 1 cm. long and about 4 mm. wide, flat, setose, 1- to 3-jointed, the joints separating from the margins in age.

Mexico to Panama.

PANAMÁ: Pearl Islands, San José Island, *I. M. Johnston 177, 818, 818A.*

The Johnston collections constitute a new record from Panama for this interesting species, concerning which I. M. Johnston is publishing notes elsewhere (in mss. as this is written). The species is the smallest, least offensive of any of the genus in Panama, and is not apt to be confused with other species except perhaps *M. pudica.* I have not had opportunity to examine the type of the species, but there seems little doubt that the name applies to the Panama collections. The Colombian *M. martensis* Britt. & Rose may be a more pubescent variety of *M. pusilla.*

8. MIMOSA INVISA Mart. in Flora 20:Beibl. 2:121. 1837.

Schrankia brachycarpa Benth. in Hook. Jour. Bot. 2:130. 1840, fide Benth.
Mimosa diplotricha C. Wright in Sauvalle, An. Acad. Habana 5:405. 1896, fide Britt. & Rose.
Morongia pilosa Standl. in Contr. U. S. Nat. Herb. 18:105. 1916, fide Britt. & Rose.
Schrankia pilosa Macbride, in Contr. Gray Herb. 59:11. 1919.

Herb or small shrub, prostrate, decumbent or scandent, the branchlets strongly angled, subtetragonal, usually lightly pilose (sparingly so on older twigs especially), copiously armed with recurved thorns. Leaves reportedly sensitive, moderate, bipinnate, the pinnae mostly 4–7 pairs opposite on the rachis, the leaflets several to many (usually about 15–20) pairs per pinna; petiole elongate, 2–5 cm. long, characteristically exceeding the rachis, eglandular, pulvinate, aculeate; rachis equalling or almost equalling and similar to the petiole, bearing setiform appendages at insertion of the pinnae; pinnae comparatively remote, mostly 2–3 cm. long, bearing just above the pulvinus usually paired, setiform appendages; leaflets linear or linear-oblong, 2–5 mm. long and about 1 mm. wide, bluntly acute or subobtuse apically, inequilaterally rounded or subtruncate basally, lightly pubescent or subglabrous, the costa visible but secondary venation obscure; stipules setiform, about 4 mm. long. Inflorescence of pedunculate heads solitary to few-fasciculate from older foliate and subterminal non-foliate nodes; peduncles normally no more than 1 cm. long, aculeate and usually sparingly pubescent; heads compact, globular, several- to many-flowered; floral bractlets oblanceolate, about 1 mm. long, glabrous. Flowers sessile, pink; calyx cupular, much less than 1 mm. long, glabrous; corolla funnelform, 2–3 mm. long, glabrous, 4-lobed, the lobes about equalling the tube;

Fig. 100. *Mimosa somnians*

stamens 8, about 6 mm. long, the filaments thickish, the anthers about ½ mm. long; ovary short, verrucose laterally, the style equalling the stamens, the stigma narrow. Legume oblong, usually less than 2 cm. long and about 5 mm. wide, flat, segmented, normally pilose, the persistent margins setose-spinose.

Mexico to Argentina; West Indies.

BOCAS DEL TORO: Almirante, *Rowlee & Stark 498*. CANAL ZONE: Corozal, *Standley 27368*; Summit, *Standley 26951*. PANAMÁ: Chepo, *Pittier 4544*; Juan Franco Race Track, *Standley 27798*. PROVINCE UNKNOWN: Las Delicias, *Carleton 41*.

Mimosa invisa is on the "continental divide" between *Mimosa* and *Schrankia;* vegetative and floral appearance is that of *Schrankia,* but the comparatively broader legume necessitates inclusion in *Mimosa*. The species is another "sensitive plant" or *dormilona,* rather easily distinguishable from *M. pudica* by the comparative remoteness of the pinnae. The plant frequently invades cleared areas, where it becomes an objectionable weed, potentially a source of severe lacerations to the unwary. Pittier reports various parts or infusions of the plant to be both mildly toxic and medicinal. *M. invisa* has a great many expressive local names, such as *malicia de mulher* in eastern Brazil and *raspacanilla* in lower Central America.

9. MIMOSA SOMNIANS Humb. & Bonpl. ex Willd. Sp. Pl. 4:1036. 1806.

Mimosa palpitans H. & B. ex Willd. loc. cit. 1806, fide Benth.
Mimosa somniculosa HBK. Nov. Gen. & Sp. 6:257. 1824, fide Benth.
Mimosa acutiflora Benth. in Hook. Jour. Bot. 4:397. 1842, fide Benth.
Mimosa podocarpa Benth. loc. cit. 1842, fide Benth.
Mimosa quadrijuga Salzm. ex Benth. loc. cit. 398. 1842, fide Benth.

Decumbent or nearly erect or even subscandent herb or subshrub, the branchlets subterete, longitudinally striate, usually pilose with gland-tipped hairs, sparingly or moderately aculeate with broad-based, recurved thorns. Leaves moderate, bipinnate, the pinnae usually about 4 (2–8) pairs opposite on the rachis, the leaflets many (20 more or less) pairs per pinna; petioles moderate, 1–3 cm. long, normally shorter than the rachis, armed and pubescent like the branchlets, otherwise eglandular; rachis 1.5–8 cm. long, like the petiole but less pubescent, bearing a subulate appendage at insertion of each pair of pinnae; pinnae 1–4 cm. long, setose-spinose particularly on the pulvinus; leaflets broadly linear, 2–5 mm. long and usually less than 1 mm. wide, rounded or obtuse apically, obliquely subtruncate basally, glabrous or sparingly puberulent, the venation obscure except for the costa; stipules lanceolate-subulate, about 5 mm. long, pubescent. Inflorescence of pedunculate heads solitary or few-fasciculate from both non-foliate subterminal nodes and lower foliate nodes, thus appearing racemose distally; peduncles up to 3 cm. long in age, most frequently glabrous; heads globular, compact; floral bractlets ovate-lanceolate, about 1 mm. long, ciliate. Flowers sessile, pink; calyx minute, much less than 1 mm. long; corolla funnelform, about 3 mm. long, glabrous, markedly striate, the 4 lobes about equalling the tube, subrigid and pointed in bud; stamens 8, about 7 mm. long, glabrous, the filaments somewhat thickish. Legume narrowly linear,

4–7 cm. long and about 4 mm. wide, flat, several-segmented, stipitate, usually glandular-pubescent and setose when young, less prominently so in age, the persistent margins short aculeate-setose.

Mexico to Argentina.

CANAL ZONE: Balboa, *Standley 26063;* Fort Kobe Road, *Woodson, Allen & Seibert 1410.* CHIRIQUÍ: Boquete, *Woodson & Schery 796; Pittier 3321.* COCLÉ: El Valle de Antón, *Allen 470, 2817.* PANAMÁ: without data, *M.B.G. 1090295;* "Sabanas", *Bro. Paul 57;* Tumba Muerto Road, *Standley 29770.* PROVINCE UNKNOWN: without locality, *Seemann 105.*

This species is rather well distinguished by the glandular pubescence (usually) and striate corolla. Along with certain other species it seems to bear the common name *dormilona* in Central America, indicating that it too is a "sensitive plant" responding visibly to contact or other stimuli. It seems to prefer open, moist, often sandy habitats at moderate elevations.

10. MIMOSA PIGRA L. Cent. Pl. in Amoen. Acad. 4:274. 1755.

Mimosa asperata L. Syst. Nat. ed. 10, 1312. 1759.
Mimosa polyacantha Willd. Sp. Pl. 4:1034. 1806, fide Benth.
Mimosa hispida Willd. loc. cit. 1037. 1806, fide Benth.
Mimosa canescens Willd. loc. cit. 1038. 1806, fide Benth.
Mimosa pellita H. & B. ex Willd. loc. cit. 1037. 1806, fide Benth.
Mimosa ciliata Willd. Enum. Hort. Berol. 1048. 1809, fide Benth.
Bentham also lists other African and Far Eastern synonyms.

Shrub to a few meters tall, sometimes scandent, the branchlets usually conspicuously setose-hispid and armed with formidable recurved thorns. Leaves reported sensitive, moderate to large, bipinnate, the pinnae up to 15 or even more pairs opposite on the rachis, the leaflets usually about 25 or 30 pairs per pinna; petiole comparatively short, seldom more than 1 or 2 cm. long, eglandular, hispid like the twigs, usually aculeate; rachis 4–25 cm. long, similar to the petiole, eglandular, the thorns frequently becoming acicular; pinnae 2–7 cm. long, hispid; leaflets linear, 2–8 mm. long and approximating 1 mm. in width, acute apically, inequilaterally rounded or subtruncate basally, appressed-pubescent (especially below) and setose-ciliate margined, longitudinally few-veined, these veins prominent below; stipules ovate-lanceolate, as much as 8 mm. long, pubescent. Inflorescence of solitary or few-fasciculate, pedunculate heads, axillary from foliate and subterminal non-foliate nodes; peduncles up to 5 cm. long in age, hispid; head ovoid, dense; floral bractlets linear, 2–3 mm. long, pectinate above the middle. Flowers sessile, whitish; calyx tubular, about 2 mm. long, cleft to one side, laciniate apically, glabrous; corolla funnelform, about 4 mm. long, short-hispid apically, the 4 lobes less than ½ the length of the tube; stamens 8, free, the filaments scabrous and expanded distally; ovary setose-hispid. Legume linear-oblong, mostly 4–7 cm. long and little more than 1 cm. wide, short-beaked, stipitate, flat, 7- to 20-segmented, densely hispid-setose both on the persistent margins and on the segments.

Mexico to Brazil and Peru; West Indies; Africa and Far East (introduced?).

CANAL ZONE: "Chagres", *Fendler 98;* Frijoles, *Bro. Heriberto 84.* COCLÉ: Penonomé, *Williams III.* PANAMÁ: between Panamá and Chepo, *Dodge, Hunter, Steyermark & Allen 16684; Bro. Maurice 761;* Tumba Muerto Road, *Standley 29832.*

The species is distinctive except in Mexico where a smaller, less pubescent form has been regarded as a separate species (*M. Berlandieri* A. Gray) or variety (var. *Berlandieri* (Gray) Robins.). The heavy, coarse pubescence and multipinnular leaf serve to distinguish it from other species through most of its range. *M. pigra* is said to be almost as sensitive as the renowned *M. pudica,* contracting its leaves quickly when disturbed. It bears, as does *M. pudica,* the expressive local name of *dormilona* as well as *pica-pica* in lower Central America, where it is a common weed of moist but open lowland areas.

8. SCHRANKIA Willd.

SCHRANKIA Willd. Sp. Pl. 4:1041. 1806, not Medic. 1792; nom. conserv.

Leptoglottis DC. Mem. Legum. 451. 1825.
Morongia Britt. in Mem. Torrey Bot. Club 5:191. 1894.

Perennial herbs or subshrubs, often decumbent or clambering, armed with recurved thorns, the branchlets usually markedly angulate. Leaves moderate or moderately small, bipinnate, usually sensitive, the pinnae few or several remote pairs opposite on the rachis, the leaflets several to many pairs per pinna; petiole comparatively elongate, in many species exceeding the rachis, aculeate, eglandular; rachis similar to the petiole, eglandular but with subulate appendages at insertion of pairs of pinnae; pinnae usually bearing a pair of bract-like mucrons just above the basal callus; leaflets small, usually inequilateral basally, the venation obscure or less frequently prominent; stipules linear-subulate, arcuate, subpersistent. Inflorescence of axillary, pedunculate heads; peduncles short (most South American species) or moderately elongate (many Mexican and North American species); heads dense, globular; bractlets small, concave but not peltate. Flowers small, essentially sessile, mostly 5-merous, pinkish, the upper ones perfect, the lower ones usually staminate; calyx small, nearly campanulate, prominently toothed, usually glabrous; corolla funnelform-campanulate, sympetalous, the teeth or lobes prominent, usually glabrous; stamens 8–13 (usually 10), free (except perhaps at base), exserted; anthers small, ovate-orbicular, eglandular; ovary nearly symmetrical, usually glabrous, several- to many-ovulate, briefly stipitate; style about equalling the stamens; stigma terminal, not expanded. Legume narrowly linear, terete or at least turgid, usually aculeate, not jointed, the face of the valves separating from the margins in dehiscence (thus at length longitudinally 4-valvate), usually with a brief or elongate acuminate beak; seeds longitudinal, oblong, obliquely truncate, blackish.

Temperate and tropical North America to middle South America; West Indies; introduced into Africa, Pacific Islands, and Far East.

Schrankia is a small genus, distinguishable from *Mimosa* only with difficulty, and reliably only in mature fruit. Except that *Schrankia* has been traditionally separated from *Mimosa*, there seems little more justification in recognizing it than a great many Britton & Rose segregate genera not commonly accepted. As is typical of most genera of the MIMOSOIDEAE, species within the genus are not clear-cut. Of the 27 species listed by Britton & Rose (N. Am. Fl. 23:138–144) only a fraction are likely tenable. Two species are reported to occur in Panama, probably both of them "good" but possibly grading into "species" of Mexico and the United States.

a. Pinnae mostly 2–3 pairs; venation of leaflet except for the costa obsolete; legume about 4 mm. wide, long-beaked ..... 1. S. LEPTOCARPA
aa. Pinnae mostly 4–5 pairs; leaflet venation delicately reticulate below; legume 5–6 mm. wide, short-beaked ..... 2. S. HAMATA

1. SCHRANKIA LEPTOCARPA DC. Prodr. 2:443. 1825.

Leptoglottis leptocarpa (DC.) Standl. in Jour. Wash. Acad. 15:458. 1925.
?Schrankia trijuga Goyena, Fl. Nic. 1:379. 1909.

Perennial, subherbaceous plant, decumbent, straggling or somewhat scandent; branchlets lightly to heavily armed with recurved thorns, glabrous, angled or subtetragonal. Leaves moderate but slender and lax, bipinnate, the pinnae mostly 2–3 pairs (rarely 1 or 4–5 pairs), the leaflets ordinarily about 10–15 pairs per pinna; petiole elongate, 2–8 cm. long, subglabrous, generally armed like the branchlets, eglandular; rachis 1–4 cm. long, similar to the petiole, bearing above at insertion of the pairs of pinnae 1–2 subulate, stipule-like appendages (these sometimes caducous); pinnae 1–4 cm. long, callous basally and usually bearing there a pair of minute, bract-like mucrons; leaflets linear-oblong to narrowly obovate-elliptic, 3–10 mm. long and 1–2 mm. wide, rounded-submucronate or obtuse apically, inequilaterally rounded basally, glabrous except ciliate-margined, dull, the venation obscure; stipules linear-subulate, curved, few to several mm. long. Inflorescence of axillary, pedunculate heads; peduncles short, mostly about 1 cm. long, eglandular; heads several-flowered, orbicular, the bractlets lanceolate or oblanceolate. Flowers subsessile, pinkish; calyx campanulate, considerably less than 1 mm. long, glabrous, irregularly 5-toothed; corolla funnelform-campanulate, about 2 mm. long, glabrous, the 5 teeth almost equalling the tube; stamens 10, about 6 mm. long, free, glabrous, the anthers ovate-orbicular; ovary substipitate, verrucose. Legume linear, up to 12 cm. long, acuminate-subulate, moderately aculeate, the thorns in 3 rows on each margin with an additional row on each valve, subglabrous, the valves separating from the margins in dehiscence.

Central America and West Indies to middle South America; introduced into Old World tropics.

CANAL ZONE: Ancón, *Pittier 6769.* COCLÉ: Aguadulce, *Pittier 4835;* Penonomé, *Williams 109.* PANAMÁ: Las Sabanas, *Bro. Heriberto 263; Standley 25935.*

Certain species of Mexico and the southern United States are remarkably similar to S. *leptocarpa*. For example, S. *Roemeriana*, a number of specimens commonly passing as S. *microphylla* (= S. *horridula*, = S. *uncinata*, = S. *angustata*), and several Small and Britton & Rose species are difficultly separable from it. Yet the name S. *leptocarpa* has priority over most possible synonyms, and will likely endure.

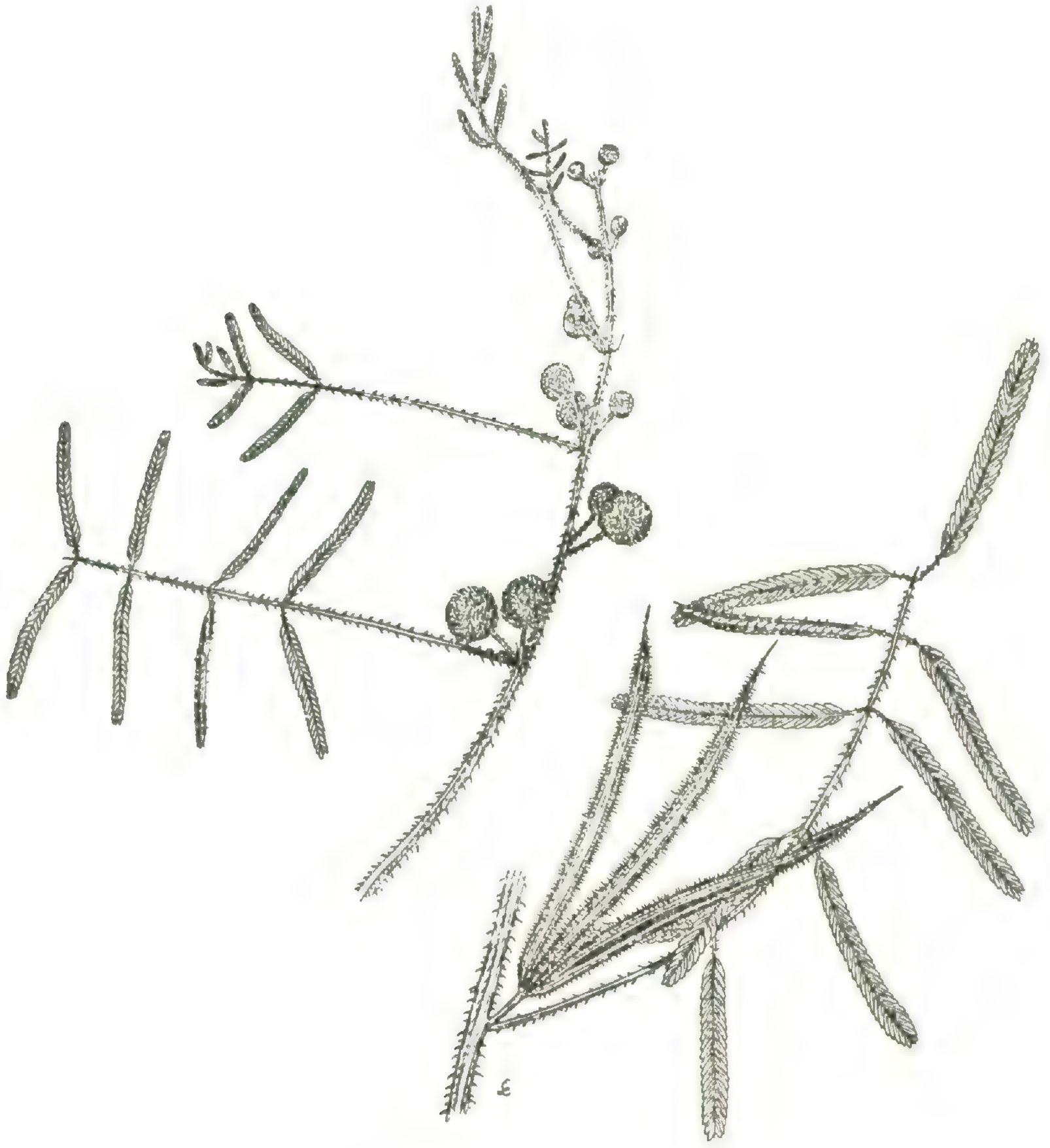

Fig. 101. *Schrankia hamata*

2. SCHRANKIA HAMATA Humb. & Bonpl. ex Willd. Sp. Pl. 4:1042. 1806.

Mimosa tetragona Poir. in Lam. Encycl. Meth. Suppl. 1:56. 1810, fide Benth.
Leptoglottis hamata Standl. in Jour. Wash. Acad. 15:458. 1925.

Slender, clambering, mostly glabrous, herbaceous plant, the branchlets pentagonal and copiously armed on the ridges with recurved thorns. Leaves bipinnate, the pinnae usually 4–5 pairs, the leaflets mostly 10–20 pairs; petiole moderate, about 5 cm. long, it and the rachis aculeate; rachis usually exceeding the petiole, eglandular but with interpinnular mucrons; leaflets linear, up to 7 mm. long, acute

or obtuse apically, inequilaterally truncate basally, glabrous except sparingly ciliate on the margins, delicately reticulate-veined below. Peduncles axillary, about 1 cm. long, pubescent, often aculeate; head globose. Flowers small, dense, sessile; calyx campanulate, about ½ mm. long, glabrous, briefly 5-dentate; corolla funnelform, about 3 mm. long, glabrous, 5-lobate, united below for about ⅓ its length; stamens 10, about 6 mm. long, glabrous, free; anthers ovate, about ½ mm. long; ovary glabrous, briefly stipitate, multi-ovulate, angled, with the style 4–5 mm. long. Legume 6–10 cm. long and about 5 mm. wide, terete-tetragonal, heavily setose-aculeate, the beak being about 1 cm. long.

Panama and Colombia.

CANAL ZONE: Ancón, *Pittier 6863*; Balboa, *Standley 32113*; Bella Vista, *Piper 5114*. DARIÉN: Pinogana, *Allen 4277*. PANAMÁ: Corozal road, *Standley 26761*; Panamá, *Macbride 2609*; *Standley 27700*; Tumba Muerto road, *Standley 29702*.

Schrankia hamata is reported quite common in Colombia and Panama. It apparently is distinct from *S. leptocarpa* (in having a thicker, more spiny legume, larger leaves with more pinnae, and leaflets with lateral veins distinct), but may not be separable from certain Mexican species.

9. NEPTUNIA Lour.

NEPTUNIA Lour. Fl. Cochinch. 653. 1790.

Hemidesmas Raf. Sylva Tellur. 119. 1838, in part.

Generally herbs but sometimes somewhat woody, of moist or swampy ground and sometimes free-floating on ponds or quiet water, the branchlets unarmed, not lenticellate, in most species glabrous, occasionally spongy-inflated in submerged stems. Leaves usually moderate, bipinnate, the pinnae opposite, few, the pairs moderately remote, the leaflets several to many pairs, small; petiole prominent, glandular or eglandular; rachis similar to and usually approximating the petiole, eglandular; leaflets nearly linear, inequilateral basally, usually glabrous but often ciliate, the venation prominent or obscure; stipules conspicuous, often cordate-subclasping, sometimes striate-nerved. Inflorescence of axillary, pedunculate heads or very short spikes, usually solitary; peduncles elongate, commonly bearing 2 small or large bracts; heads dense, mostly obovoid, the basal flowers staminate or sterile and smaller in bud, the upper flowers perfect, larger in bud. Flowers sessile, usually yellowish, the basal ones with prominent petaloid staminodia, the perfect ones relatively inconspicuous; calyx synsepalous, more or less cupulate, 5-parted; corolla of 5 free petals or these in some cases coherent near the middle (but free below and above), usually glabrous; stamens or staminodia mostly 10, free; ovary generally glabrous, the stout style elongate and bearing an expanded stigma. Legume short and broad, flat, unarmed, 2-valved, not septate nor the valves separating from the margins, the seeds transverse.

World tropics and subtropics; in the Western Hemisphere from middle United States to Brazil.

Neptunia is a small genus, containing 6 or fewer species in the Americas. DeCandolle and others included it as a section of Desmanthus, but more recently it has been generally accepted as a distinct genus. It is unusual and distinctive in possessing basal flowers of the head with conspicuous petaloid staminodia, and in preferring aquatic or swamp habitats.

a. Stipules striate-nerved; leaflets ciliate, the venation remote but prominent below; petals coherent about at the middle; peduncular bracts borne above the middle..... 1. N. pubescens
aa. Stipules scarcely nerved; leaflets glabrous, the venation obscure; petals free; peduncular bracts borne near and below the middle, or absent.
b. Not floating, the stem seldom developing a spongy outer tissue; petiole glandular; flowers yellow..... 2. N. plena
bb. Free-floating, with a thick spongy outer tissue on the submerged stem; petiole eglandular or merely callous apically; flowers whitish?.. 3. N. prostrata

1. Neptunia pubescens Benth. in Hook. Jour. Bot. 4:356. 1842.

Neptunia floridana Small, in Bull. Torrey Bot. Club 25:138. 1898.
Neptunia Lindheimeri B. L. Robins., in Proc. Am. Acad. 33:333. 1898.
Neptunia microcarpa Rose, in Contr. U. S. Nat. Herb. 8:300. 1905.

Slender herb or subshrub, prostrate or ascending from a somewhat woody base, the branchlets terete, glabrous or pubescent. Leaves moderate or moderately small, bipinnate, the pinnae 2–4 (normally 3) pairs opposite on the rachis, the leaflets many (12–40) pairs per pinna; petiole slender, 1–2 cm. long, pubescent or glabrous, eglandular; rachis about as long as the petiole, eglandular, terminally apiculate; pinnae mostly 2–4 cm. long, moderately remote, the axis somewhat alate; leaflets linear-oblong, 3–5 mm. long and 1–2 mm. wide, obtuse apically, obliquely rounded basally, usually glabrous except for a ciliate margin, the venation prominent below but remote; stipules ovate or lanceolate, about 4–5 mm. long, prominently longitudinally striate-nerved, subpersistent. Inflorescence of solitary, axillary, pedunculate heads; peduncles elongate, up to 6 cm. long in age, usually minutely 1- to few-bracteate near or above the middle; heads globose to briefly oblong, bearing dimorphic flowers; floral bractlets lanceolate or oblanceolate, about 2 mm. long, ciliate or glabrous. Flowers of 2 (3?) types, the few lower ones of head unisexual and with conspicuous petaloid stamens or staminodia; upper flowers without petaloid stamens or staminodia, usually perfect (occasionally with pistil aborted), sessile, yellow; calyx cupulate-funnelform, about 2 mm. long in perfect flowers, somewhat shorter in basal flowers, prominently 5-lobed, the lobes usually ciliate; corolla funnelform, about 3 mm. long in perfect flowers, somewhat shorter in basal flowers, glabrous, 5-lobate, the lobes about equalling the imperfectly closed tube; stamens (or staminodia) usually 10, glabrous, 5–6 mm. long; ovary glabrous, subfusiform, the style stout and about equalling the stamens. Legume broadly oblong, mostly 2–3 cm. long and 1 cm. wide or wider, flat, rounded apically and briefly mucronate, substipitate basally, 2-valved, few-seeded, glabrous, the seeds transverse and slightly oblique.

Florida to Texas and Mexico; West Indies; southern Central America; Peru; southern South America.

COCLÉ: Aguadulce, *Pittier 4962*.

This species is readily distinguished from others of the genus in Panama by the striate stipules, adherent petals, and ciliate leaflets with prominent venation. The species much resembles *N. lutea* of the United States.

2. NEPTUNIA PLENA (L.) Benth. in Hook. Jour. Bot. 4:355. 1842.

Mimosa plena L. Sp. Pl. 519. 1753.
Mimosa punctata L. Sp. Pl. ed. 2, 1502. 1763.
Desmanthus plenus Willd. Sp. Pl. 4:1045. 1806.
Desmanthus punctatus Willd. loc. cit. 1047. 1806.
Mimosa lycopodioides Desf. in Pers. Syn. Pl. 2:263. 1807, fide Benth.
Acacia lycopodioides Desv. in Jour. Bot. 3:68. 1814.
Desmanthus polyphyllus DC. Prodr. 2:444. 1825, fide Benth.
Acacia punctata Desf. Cat. Hort. Par. 300. 1829.
Mimosa adenanthera Roxb. Fl. Ind. 2:554. 1832, fide Benth.
Neptunia polyphylla Benth. in Hook. Jour. Bot. 2:129. 1840.
Neptunia surinamensis Steud. in Flora 26:759. 1843, fide Benth.
Desmanthus comosus A. Rich. Ess. Fl. Cub. 475. 1845, fide Griseb.

Subprostrate or ascending subshrub of swampy habitats, the branchlets glabrous, not lenticellate. Leaves moderately small, bipinnate, the pinnae 2–4 (mostly 3) pairs opposite on the rachis, the leaflets 10–25 pairs per pinna; petiole 1–2 cm. long, glabrous, somewhat flattened above, bearing a sessile, orbicular gland apically just below insertion of lowermost pair of pinnae; rachis 1–4 cm. long, similar to the petiole, eglandular (except for gland already noted at apex of petiole), terminally apiculate; pinnae 1–5 cm. long, the pairs moderately remote from one another; leaflets linear or linear-spatulate, 3–10 mm. long and 1–2 mm. wide, rounded or obtuse and usually very briefly mucronate apically, obliquely subtruncate basally, glabrous, all venation obscure; stipules obliquely ovate-lanceolate and subclasping, usually about 5 mm. long. Inflorescence of axillary, pedunculate heads or very short spikes; peduncles up to 10 cm. long in age, glabrous, conspicuously bibracteate below the middle; heads dense, the floral bractlets obovate-lanceolate, little more than 1 mm. long. Flowers sessile, yellow, the upper ones perfect, the lower ones staminate or infertile and with 10 conspicuous petaloid staminodia 7–8 mm. long; calyx cupulate, about 1 mm. long, 5-lobed, glabrous; corolla of 5, free, spatulate petals about 3 mm. long, glabrous; stamens 10?, 4–5 mm. long, glabrous, the anthers almost 1 mm. long; ovary glabrous, dark; style stout, exceeding the stamens; stigma expanded, truncate. Legume oblong, 2–4 cm. long and about 1 cm. wide, apiculate, flat, glabrous, conspicuously stipitate, 2-valved, the seeds several, transverse.

Mexico and Guatemala, West Indies, Panama and Colombia to Brazil.

COCLÉ: Penonomé, *Williams 97*.

This species characteristically grows in marshy, open areas such as the shallow ponds of the savannas. *N. plena* can be distinguished rather readily from other species of *Neptunia*, except *N. prostrata*, by a variety of characters. However, occasionally plants appearing identical with *N. plena* (or other species) will develop the thick, fleshy, floating stems characteristic of *N. prostrata*. This stem characteristic has been the chief means of distinguishing *N. prostrata*.

3. Neptunia prostrata (Lam.) Baillon, in Bull. Soc. Linn. Paris 1:356. 1883.

Mimosa prostrata Lam. Encycl. Meth. 1:10. 1783.
Neptunia oleracea Lour. Fl. Cochinch. 654. 1790.
Mimosa natans Vahl, Symb. 3:102. 1794 (L.f. Suppl. 439. 1781. = nomen nudum).
Mimosa lacustris H. & B. Pl. Aequin. 1:55. 1806.
Desmanthus lacustris Willd. Sp. Pl. 4:1044. 1806.
Desmanthus natans Willd. loc. cit. 1806.
Mimosa aquatica Pers. Syn. Pl. 2:263. 1807, fide Benth.
Desmanthus stolonifer DC. Prodr. 2:444. 1825, fide Benth.
Acacia lacustris Desf. Cat. Hort. Paris, 301. 1829.
Neptunia stolonifera Guill., Perr. & Rich. Fl. Seneg. 239. 1830–33.

Prostrate, floating herb or "subshrub," the submerged stems spongy-inflated with a pithy outer surface, bearing nodular roots, the above-water stems glabrous, flexuous, not lenticellate. Leaves moderate, 2-ranked, bipinnate, the pinnae mostly 3 pairs opposite on the rachis, the leaflets usually about 15 pairs per pinna; petioles mostly 2–3 cm. long, glabrous, somewhat flattened above, eglandular or with an apical callus just below insertion of the basal pair of pinnae; rachis similar to and approximating the petiole; pinnae usually 2–4 cm. long, the pairs moderately remote from one another, glabrous; leaflets linear or linear-spatulate, 3–12 mm. long and 1–3 mm. wide, rounded or obtuse and often briefly mucronulate apically, obliquely rounded or subtruncate basally, glabrous, the venation obscure; stipules inequilaterally ovate-lanceolate, generally about 5 mm. long, glabrous, not striate. Inflorescence of axillary, pedunculate heads or very short spikes; peduncles elongate, as much as 15 cm. long, glabrous, usually bearing near or below the middle 2 rather small bracts; heads obovoid in bud, dense, bearing staminate or infertile flowers basally and perfect flowers apically. Flowers sessile, bi-(tri?)-morphic, reportedly whitish fading yellow; calyx of perfect flowers, cupulate-funnelform, about 2 mm. long (smaller in basal flowers), glabrous, 5-lobed; corolla of 5 linear-spatulate petals, about 4 mm. long, glabrous; stamens of perfect flowers about 10, 7–8 mm. long; staminodia of basal flowers normally 10, petaloid, as much as 15 mm. long, glabrous; ovary glabrous; style exceeding the stamens; stigma expanded, truncate. Legume oblong, 10–25 mm. long and about 8 mm. wide, flat, somewhat curved, stipitate, briefly beaked, glabrous, few-seeded, the seeds transverse.

World tropics. In Western Hemisphere: Mexico and Guatemala, West Indies, Panama and Colombia to Peru and Brazil.

Coclé: Aguadulce, *Woodson, Allen & Seibert 1209.*

There is some question as to whether the cited specimen may more properly

belong to this species or to *N. plena.* The floating nature of the spongy, inflated stem, however, warrants its inclusion as *N. prostrata.* Probably *N. prostrata* is not a valid species, but merely a form of *N. plena* growing floating in water and assuming a prostrate position.

10. DESMANTHUS Willd.

DESMANTHUS Willd. Sp. Pl. 4:1044. 1806, nom. conserv.
Acuan Medik. Theodora, 62. 1786.
Darlingtonia DC. in Ann. Sci. Nat. Bot. 4:97. 1825.
Acuania Ktze. Rev. Gen. Pl. 1:158. 1891.

Perennial, small, usually diffuse or decumbent shrubs, or subherbaceous. Leaves moderately small, bipinnate, the pinnae one to many pairs opposite on the rachis, the leaflets few or many pairs, opposite; petiole short, either it and/or the rachis bearing one or more subcupular glands, very rarely eglandular; leaflets small, obscurely veined in most species, glabrous or infrequently pubescent; stipules setiform. Inflorescence of axillary, pedunculate heads, the peduncle usually slender; head dense, usually few-flowered, the flowers more or less erect and the head then less than hemispherical; floral bracts nearly lanceolate, apparently never peltate as in most species of *Leucaena.* Flowers small, sessile, whitish or greenish; calyx synsepalous, more or less campanulate, 5-dentate; corolla essentially polypetalous, 5-parted, valvate, the petals narrowed basally; stamens 5 or 10 (staminodes 5 or 0), free, normally exceeding the perianth; anthers comparatively larger as in *Leucaena,* not smaller as in *Acacia,* eglandular; ovary subsessile, bilateral, several-ovulate, usually glabrous; style thickened above into a truncate-concave stigma. Legume small, linear, flat, 2-valved, straight or curved, sometimes somewhat constricted between the seeds, dehiscent from the apex (the rather thin, dehisced valves subpersistent), subseptate or continuous; seeds usually oblique, compressed.

Temperate, subtropic and tropic regions of the New World; introduced into the Old World.

Desmanthus is obviously close to *Leucaena,* the basic floral and fruit characters being almost identical. However, whereas *Leucaena* consists chiefly of arborescent species, species of *Desmanthus* are small shrubs or subherbaceous. In Central America additional characters serve to rather readily separate these genera, the more obvious of which are used in the key to the genera.

Desmanthus is a small genus, but exceedingly troublesome from the standpoint of specific delimitation. As collections have accumulated it has become apparent that many of the characters on which species had been formulated do not hold constant, and that intergradation is rampant between almost all "species." Two specimens may appear distinct, but usually "connecting" specimens exhibiting all degrees of intergradation can be found to link them. Thus, for practical reasons, if no other, not more than a handful of species appear worthy of recog-

nition, and even these may not be readily distinguishable. On the basis of general observation of the genus the three "species" reportedly occurring in Panama are here combined under the oldest name, which thus considered is the only species known from Central America.

1. Desmanthus virgatus (L.) Willd. Sp. Pl. 4:1047. 1806.

Mimosa virgata L. Sp. Pl. 519. 1753.
Mimosa pernambucana Mill. Gard. Dict. ed. 8, no. 3. 1768, not L., fide Britt. & Rose.
Mimosa angustisiliqua Lam. Encycl. Meth. 1:10. 1783.
Acuan virgatum Medik. Theodora, 62. 1786.
Acacia virgata Gaertn. Fr. & Sem. 2:317. 1791.
Desmanthus depressus H. & B. ex Willd. Sp. Pl. 4:1046. 1806.
Desmanthus diffusus Willd. loc. cit. 1806.
Mimosa depressa Poir. in Lam. Encycl. Meth. Suppl. 1:58. 1810.
Desmanthus strictus Bertol. Giorn. Arcad. 21:190. 1824.
Desmanthus leptophyllus HBK. Nov. Gen. & Sp. 6:264. 1824, fide Benth.
Desmanthus tenellus DC. Prodr. 2:445. 1825.
Acacia angustisiliqua Desf. Cat. Hort. Paris, ed. 3, 300. 1829.
Desmanthus pratorum Macf. Fl. Jam. 1:311. 1837.
Acacia depauperata Mart. in Steud. Nom. Bot., ed. 2, 4. 1841, fide Benth.
Desmanthus virgatus strictus Griseb. Fl. Br. W. Ind. 218. 1860.
Acacia leptosperma Bello, in Anal. Soc. Esp. Hist. Nat. 10:265. 1881.
Acuan depressum Ktze. Rev. Gen. Pl. 1:158. 1891.
Acuan latum Britt. & Rose, in N. Am. Fl. 23:132. 1928.
Acuan bahamense Britt. & Rose, loc. cit. 1928.
Acuan insulare Britt. & Rose, loc. cit. 133. 1928.

Small shrub or subherbaceous, nearly erect or more commonly diffuse or decumbent, the branchlets essentially glabrous, angled or subtetragonal, scarcely lenticellate. Leaves moderately small, bipinnate, the pinnae 1–7 (mostly 2–4) pairs opposite on the rachis, the leaflets mostly 10–20 pairs per pinna; petiole usually no more than 5 mm. long, subterete, perhaps ciliate above, bearing apically at insertion of the lowermost pair of pinnae a large or small, orbicular to obovate, cupulate or patelliform, sessile gland; rachis usually flattened and lightly pubescent or ciliate above, eglandular (except for gland already described at juncture of rachis and petiole), apiculate from the lower side apically; pinnae 1–4 cm. long; leaflets linear or linear-oblong, 2–8 mm. long and mostly 1–2 mm. wide, obtuse or rounded apically, obliquely truncate basally, glabrous except usually ciliate, the costa but not secondary veins visible; stipules setiform, mostly 3–5 mm. long. Inflorescence of axillary, pedunculate heads towards the tips of the twigs; peduncles up to 6 cm. long (in age), usually scatteringly pubescent; head small, dense, few-flowered, the flowers all erect; floral bractlets lanceolate, about 2 mm. long, subrigid. Flowers whitish, sessile; calyx cupular-tubular, 2–3 mm. long, glabrous or subglabrous, prominently dentate; corolla of 5 essentially free, obovate, glabrous petals 3–4 mm. long; stamens 10, free, glabrous, the filaments 6–7 mm. long; anthers ovate, almost 1 mm. long, glabrous; ovary linear-oblong, about 3 mm. long, curved, glabrous, bilateral; style about 5 mm. long, expanded apically into a truncate stigma. Legume linear, mostly 4–6 cm. long and 3–4 mm. wide, flat, glabrous, short-beaked, dehiscent on both valves, the seeds oblique.

Florida and Texas to Argentina; West Indies; Galapagos; probably introduced elsewhere.

CANAL ZONE: Balboa, *Standley 27137, 32146.* COCLÉ: Aguadulce, *Pittier 4970.* PANAMÁ: Matias Hernández, *Pittier 6906;* Las Sabanas, *Standley 30693; Bro. Paul 598.*

A fairly common but inconspicuous weedy plant in Central America, generally flowering during the rainy season.

Standley and Steyermark, following Fawcett and Rendle, have recently recognized the synonymity of *D. depressus* and *D. virgatus.* My observations similarly indicate that no reasonably distinct boundary exsits between these two species. Perhaps *D. depressus* could be profitably reduced to varietal status under *D. virgatus,* for the name well reflects a tendency within the species-complex towards more diffuse habit, smaller (fewer pinnae) leaves, and less prominent rachial gland. However, I cannot say into which category Panamanian specimens would likely fall.

11. LEUCAENA Benth.

LEUCAENA Benth. in Hook. Jour. Bot. 4:416. 1842.

Ryncholeucaena Britt. & Rose, in N. Am. Fl. 23:130. 1928.
Caudoleucaena Britt. & Rose, loc. cit. 1928.

Unarmed shrubs or trees, glabrous or pubescent. Leaves bipinnate, the pinnae few or several pairs opposite on the rachis, the leaflets few and large or many and small; petiole evident, usually glandular; rachis pronounced, glandular or eglandular; pinnular rachis often gland-bearing; leaflets linear to ovate, pubescent or glabrous, usually dull. Inflorescence of axillary or racemose pedunculate heads; peduncles usually stout, solitary or fasciculate, ebracteate except at the base of the head; head globular, dense, the floral bractlets evident, usually peltate. Flowers valvate, white; calyx subcampanulate, markedly sympetalous but 5-toothed, usually pubescent apically; corolla of 5 narrow, essentially free petals; stamens 10, free, exserted, the anthers relatively large, pubescent or glabrous; ovary stipitate, glabrous or pubescent, inequilateral (bilaterally symmetrical), multiovulate; style thicker than the filaments, gradually expanded into an obliquely truncate stigma. Legume linear to oblong, straight, flat, thin, dehiscent from both margins, the seeds usually nearly transverse.

Chiefly New World tropics and subtropics; a few species described from the Far East, and some introduced into various parts of the world.

This comparatively small genus, a well recognized segregate of *Acacia,* superficially resembles *Albizzia.* The flowers, however are very different from those of *Albizzia,* and afford the diagnostic criteria for the genus. Only two species are known from Panama.

a. Leaflets small, sublinear, 8–15 mm. long, about 15 pairs per pinna..... 1. L. GLAUCA
aa. Leaflets larger, nearly ovate, 15–40 mm. long, about 4 pairs per pinna.... 2. L. MULTICAPITULA

1. Leucaena glauca (L.) Benth. in Hook. Jour. Bot. 4:416. 1842.

Mimosa glauca L. Sp. Pl. 520. 1753.
Mimosa leucocephala Lam. Encycl. Meth. 1:12. 1783.
Acacia glauca Willd. Sp. Pl. 4:1075. 1806.
Acacia leucocephala Link, Enum. 2:444. 1822.

Shrub or tree, the branchlets tomentulose becoming less pubescent in age, moderately lenticellate. Leaves large, bipinnate, the pinnae 5–10 pairs opposite on the rachis, the leaflets about 15 pairs per pinna; petioles mostly 3–4 cm. long, puberulent, sulcate or flattened above, usually bearing a sessile, conic gland apically just below insertion of the basal pair of pinnae, but this frequently absent; rachis up to 15 cm. long or longer, similar to the petiole, eglandular; pinnae up to 10 or 12 cm. long, the pinnular rachis bearing a small, patelliform gland apically at insertion of the terminal pair of leaflets; leaflets linear-elliptic, 8–15 mm. long and 2–3 mm. wide, inequilaterally acute or subobtuse basally, acute apically, subglabrous, dull, usually ciliate-margined, the costa (and perhaps 1–2 smaller basal veins) prominent, the secondary venation obscure; stipules small, ovate, pubescent. Inflorescence of large, pedunculate heads, 1–3 axillary from subterminal nodes; peduncles about 4 cm. long in age, stout, tomentulose; heads orbicular, dense, almost 2 cm. in diameter, the receptacle expanded. Flowers white; calyx tubular-campanulate, 1–3 mm. long, quite briefly dentate, pubescent apically; corolla of 5 free petals, these linear-spatulate, about 5 mm. long, puberulent without; stamens 10, 7–8 mm. long, glabrous, the anthers ovate-oblong, about 1 mm. long; ovary inequilateral, pubescent apically, many-ovulate; style thick, expanding gradually into a broad, obliquely truncate stigma. Legume linear, about 15 cm. long and nearly 2 cm. wide, minutely puberulent, stipitate, briefly apiculate, flat and thin, dehiscent on both margins, the seeds somewhat obliquely transverse.

Tropical America; introduced into various parts of the world.

Canal Zone: Balboa, *Allen 2756; Standley 30912.*

The species is frequently cultivated. Standley reports a widespread popular belief in Central America that consumption of this species by horses, mules, and pigs will lead to loss of their hair.

2. Leucaena **multicapitula** Schery, sp. nov.

Arbor vel frutex ramis teretibus primo tomentulosis denique subglabris; foliis magnis distichis bipinnatis, pinnis plerumque 6 vel 8, foliolis 6–10, petiolis 2–3 cm. longis tomentulosis subglabrisve 1-glanduliferis, rhachibus ca. 6 cm. longis, eglanduliferis, foliolis ovatis vel ellipticis, 15–50 mm. longis, 7–25 mm. latis, basi inequilateraliter late acutis apice plerumque acutis, supra leviter puberulentis subter dense canescenti-puberulentis; inflorescentia 3-composita, capitulis ultimis pedunculatis fasciculatis, pedunculis tomentosis bracteatis solum subtus capitulos, capitulis orbicularibus ad 1 cm. diametro crebris, bracteis peltatis; floribus parvis albis sessilibus; calyce infundibuliformi-campanulato ca. 1 mm. longo; petalis 5 linearioblongis ca. 2 mm. longis glabris; staminibus 10, liberis 3–4 mm. longis glabris,

Fig. 102. *Leucaena multicapitula*

antheris magnis pubescentibus glabrisve, ovario inaequilaterali glabro brevistipitato, stigmate oblique truncato; legumine late lineari ca. 12 cm. longo et 3 cm. lato tenui glabro.

Unarmed tree or shrub, the branchlets tomentulose when young becoming subglabrous, moderately lenticellate, terete. Leaves 2-ranked, large, bipinnate, the pinnae normally 3–4 pairs opposite on the rachis, the leaflets 3–5 (mostly 4) pairs per pinna; petiole about 2–3 cm. long, terete, tomentulose, becoming subglabrous, bearing a sessile, conic gland slightly below insertion of the lower pair of pinnae; rachis about 6 cm. long, similar to the petiole, eglandular or with a solitary gland at insertion of terminal pinnae; pinnular rachis 2–8 cm. long, puberulent or subglabrous, bearing a conic gland apically just below insertion of the terminal pair

of leaflets; leaflets ovate or elliptic, 15–50 mm. long and 7–25 mm. wide, broadly and somewhat inequilaterally acute basally, acute apically (occasionally rounded on same leaf), dull, densely canescent-puberulent below (at least in young leaflets) and to a lesser extent above, lighter below than above; stipules caducous. Inflorescence thrice compound, consisting of several terminal and subterminal racemes of few-fasciculate pedunculate heads; peduncles about 1 cm. long, tomentose, ebracteate except just below the head; head orbicular, less than 1 cm. in diameter, dense, beset (in bud) with pubescent, peltate bracts. Flowers whitish, sessile, small; calyx funnelform-campanulate, little more than 1 mm. long, puberulent on the teeth, the 5 teeth about as broad as long; corolla of 5 linear-oblong or linear-spatulate petals, these about 2 mm. long, glabrous; stamens 10, free, 3–4 mm. long, glabrous, the anthers ovate, somewhat less than 1 mm. long, pubescent or glabrous; ovary inequilateral, glabrous, short-stipitate, the style stout, the stigma obliquely truncate. Legume broadly linear, about 12 cm. long and almost 3 cm. wide, flat and thin, glabrous.

Panama.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 281*; Miraflores, *P. White 135* (Gray Herb., TYPE); *G. White 165* (Gray Herb., COTYPE). DARIÉN: Rio Chico, *Allen 4642, 5088*.

It is not clear just how closely this species is related to other South American species such as *L. canescens* Benth. and *L. trichodes* (Jacq.) Benth. or to a number of similar or little-known northern Central American and Mexican species described by Britton and Rose and others, many of them doubtfully tenable. It has been impossible, however, to find anything matching the cited specimens in the larger herbaria of the United States. The Darién specimens are somewhat different from the Canal Zone specimens, but it is not deemed wise to consider them yet another species. The species is particularly distinguished by the inflorescence, which forms a thrice-branched terminal panicle of heads. No other species of the genus possesses this very branched inflorescence, and in some cases the pedunculate heads are merely axillary. Nor is the dense but fine pubescence of the lower leaf surface in *L. multicapitula* similar to that of any other species of which I have been able to examine specimens. Most species have glabrous leaves or a looser, longer pubescence.

12. PROSOPIS L.

PROSOPIS L. Mantissa, 10. 1767.

Mitostax Raf. Sylva Tell. 120. 1838, fide Dalla Torre & Harms.
Neltuma Raf. loc. cit. 119. 1838.
Pleuromenes Raf. loc. cit. 144. 1838, fide Dalla Torre & Harms.
Spirolobium Orbigny, Voy. Amer. Merid. 7, p. 1, Sert. Patagon., *t. 13*. 1839, fide Dalla Torre & Harms.
Algarobia Benth. Pl. Hartweg. 13. 1839.
Strombocarpa Engelm. & Gray, in Bost. Jour. Nat. Hist. 5:243. 1845.
Sopropis Britt. & Rose, in N. Am. Fl. 23:182. 1928.

Trees or shrubs, armed or rarely unarmed. Leaves bipinnate, the pinnae 1 to several pairs, opposite, the leaflets few or many pairs per pinna; petiole prominent, usually glandular; rachis present or obsolete; leaflets generally small, glabrous or less frequently pubescent; stipules small, caducous, modified as spines, or in some species apparently lacking. Inflorescence of axillary, pedunculate heads, spikes, or even racemes. Flowers small, 5-parted, sessile or substipitate, yellowish or whitish; calyx synsepalous, usually shallowly and distantly dentate; petals free or connate near the middle; glabrous or pilose within; stamens normally 10, free, exserted; anthers comparatively large, bearing terminally a small or moderate, often caducous gland; ovary pubescent or glabrous, the style stout, the stigma small. Legume very variable, linear to spiral, flat or turgid, indehiscent, with a pulpy mesocarp, the endocarp septate or not septate.

Chiefly New World from United States to Patagonia; a few species are Asiatic or African.

A polymorphic genus, very variable and difficult to delimit precisely, containing many intergrading and difficultly distinguishable species. The genus exhibits a wide range of legume forms, which ordinarily in the MIMOSOIDEAE would be occasion for generic segregation. Strangely there has been a minimum of such segregation by responsible taxonomists, and some of the segregates (as *Strombocarpa,* here included among the synonyms) appear to merit generic consideration. Within *Prosopis* in the broad sense are found characteristics prominent among a number of different genera: hence it is not surprising to find species now accepted as *Prosopis* having been described or included in *Mimosa, Acacia, Desmanthus,* etc.

Neither the limits of the genus nor of most of the species have been accurately defined. Bentham (Trans. Linn. Soc. 30:376–388) listed 16 species in 4 sections. Burkart (Darwiniana 4:57–128) recognizes 33 species and an additional 2 sections. Britton and Rose (N. Am. Fl. 23:184–187) list 14 species (in segregate genus *Neltuma*) as occurring north of South America, but it is generally conceded that few of these are tenable. Recent opinion indicates that but a single species occurs in Panama and all Central America.

1. PROSOPIS JULIFLORA (Sw.) DC. Prodr. 2:447. 1825.

Mimosa juliflora Sw. Prodr. Veg. Ind. Occ. 85. 1788.
Mimosa piliflora Sw. Fl. Ind. Occid. 2:986. 1800, fide Burkart.
Acacia juliflora Willd. Sp. Pl. 4:1076. 1806.
Neltuma juliflora Raf. Sylva Tell. 119. 1838.
Algarobia juliflora Benth. ex Heynhold, Nom. Bot. Hort. 2:18. 1840, fide Britt. & Rose.
Neltuma Bakeri Britt. & Rose, in N. Am. Fl. 23:185. 1928.
Bentham lists 29 additional synonyms for this species (Trans. Linn. Soc. 30:377. 1875), including (under a diversity of the generic names above given) the following specific epithets: *affinis, bracteolata, cumana, cumanensis, diptera, dominguensis, dulcis, flexuosa, fruticosa, furcata, glandulosa, horrida, inermis, laevigata, odorata, pallida, salinarum, siliquastrum.*

Small shrub to moderate tree, the branchlets terete, glabrous, flexuous, obscurely lenticellate, usually armed at the "nodes" with prominent paired spines up

to a few cm. long. Leaves arising from very condensed short-shoots, moderate or moderately large, bipinnate, the pinnae mostly 1–2 pairs, opposite, the leaflets few to many pairs per pinna; petiole prominent, most frequently 2–5 cm. long, terete but flattened above, normally bearing a small, sessile, subconic gland apically above; rachis shorter than the petiole or obsolete, glabrous, apiculate terminally from below; pinnae 3–10 cm. long, the rachis glandular at the distal 1 to few rachial nodes; leaflets linear to oblong, 5–20 mm. long and 1–5 mm. wide, usually rounded or obtuse apically and basally, scarcely inequilateral, dull, glabrous or subglabrous, the venation remote and moderately prominent below; stipules linear, subsetiform. Inflorescence a slender, elongate, briefly pedunculate, axillary spike inserted on the short-shoots; peduncles mostly 1–2 cm. long, often sparsely pubescent and minutely bracteate above the middle; spike commonly about 6 cm. long, rather densely flowered, the floral bracts minute. Flowers sessile, whitish; calyx cupular, about 1 mm. long, glabrous or pubescent, the 5 teeth narrow and remote; petals 5, sublinear, 2–3 mm. long, free (at least in age), pilose within especially distally; stamens normally 10, up to 6 mm. long, free, glabrous; anthers ovate, less than 1 mm. long, gland-tipped (gland often caducous); ovary pubescent; style stout, exceeding the stamens. Legume linear or linear-subtorulose, not uncommonly 20 or more cm. long and 8 mm. wide or wider, flattened or turgid, pulpy, indehiscent.

In a broad sense United States to Argentina; in narrow sense West Indies, Venezuela, and Colombia.

PANAMÁ: Bella Vista, *Standley 25391; Maxon & Valentine 6958;* Panama Vieja, *Allen 824.* DARIÉN: La Palma, *Pittier 6616.*

This species is said to be the only one of the genus in Central America. Specific delimitation is exceedingly uncertain, and this difficulty is reflected in the unusually large number of synonyms which have accumulated. Certainly tremendous variability in vegetative and legume characters is readily discernible in any folder of "*Prosopis juliflora*" in any herbarium collection. Bentham could find no defining characters within the complex, and hence regarded the species very broadly. More recently Burkart (Darwiniana 4:105. 1940) has concluded that delimitation in the past has been excessively broad, and regards the species in a much stricter sense. However, Standley and Steyermark, with wide experience in the flora of the Americas, question (Fieldiana: Bot. 24:87. 1946) whether *P. juliflora* can even be separated from the older *P. chilensis* (Molina) Stuntz of southern South America. Certainly herbarium sheets labeled *P. chilensis* seem, at least upon superficial examination, to fall within the limits of variability exhibited by sheets labeled *P. juliflora.*

The species, whatever may eventually prove to be its correct name and specific boundaries, is a locally important plant of xerophytic and subxerophytic regions. In Central America it seems confined to thickets on the Pacific slopes where a marked dry season is usually to be had. It there may reach proportions of a small tree. In its broad sense it is better known, however, as the *mesquite* of northern Mexico and the southwestern United States, where it is usually of smaller propor-

tions. A great many common names are had for the species, among which are found *cashaw* and *algarroba*. The stem and roots provide wood for fuel, or occasionally for fence-posts, cross-ties, etc. The wood is reported to finish well, and to be resistant to decay. The pods are pulpy, and the pulp after drying and grinding forms an edible meal said to be consumed by Mexican Indians. The pods are excellent for feeding stock. In addition, the plant reportedly provides excellent honey-flowers, a tannin from the bark, and a gum from the trunk.

13. STRYPHNODENDRON Mart.

The genus *Stryphnodendron* Mart. (Flora 20:Beibl. 2:117. 1837) is known both from Costa Rica and Colombia, and well may occur in Panama although no record from there has as yet become known. The genus consists of unarmed trees, with large, bipinnate leaves and mostly alternate leaflets. The inflorescence is of axillary spikes, the flowers having 10 stamens and gland-tipped anthers. It is similar to *Prosopis* in having an indehiscent legume.

14. PIPTADENIA Benth.

PIPTADENIA Benth. in Hook. Jour. Bot. 4:334. 1842.

Stachychrysum Boj. Hort. Maurit. 114. 1837, fide Ind. Kew.
Goldmania Rose ex Micheli, in Mem. Soc. Bot. Genéve 34:274. 1903, fide Britt. & Rose.
Niopa Britt. & Rose, in Addisonia 12:37. 1927.
Pityrocarpa Britt. & Rose, in N. Am. Fl. 23:190. 1928.

Shrubs or trees, erect or sometimes decumbent, the branchlets pubescent or glabrous, aculeate or unarmed. Leaves usually large, bipinnate, the pinnae usually several, multifoliolate, both the pinnae and leaflets usually opposite; petiole normally bearing one or more sessile glands; rachis glandular or eglandular at the pinnular nodes; leaflets almost invariably small; stipules usually slender, caducous. Inflorescence of solitary or few-fasciculate, pedunculate heads or spikes, sometimes appearing paniculate by insertion at distal non-foliate nodes; floral bracts small or minute. Flowers 5-parted, sessile or subsessile; calyx more or less campanulate, the teeth commonly small, glabrous or pubescent; corolla of 5 free (or often connate to middle), narrow petals well exceeding the calyx, valvate; stamens normally 10, free except often inserted on a short tubular base or androgynophore, exserted; anthers in all except one or two species (not Panamanian) bearing an apical gland, this usually caducous in age; ovary glabrous or pubescent, often stipitate. Legume broadly linear, flat, not curved, stipitate or sessile, membranaceous or coriaceous, 2-valvate, the valve margins straight or constricted between the seeds; seeds compressed, exalbuminous.

New World tropics and subtropics; Asia and Africa.

A moderate-sized genus, abundant in middle and northern South America. It is not particularly "natural" or clear-cut, and except for the confusion that would result there might be justification in recognition of certain segregates (viz. *Niopa*).

Certain species of *Piptadenia*, at least superficially, much resemble other genera such as *Leucaena*, *Acacia*, and *Mimosa*. It thus frequently becomes difficult to identify accurately poor or incomplete specimens. The bark of some species is said to be quite astringent, and the seeds are reported highly narcotic. A single species has so far been reported from Panama.

1. Piptadenia flava (Spreng.) Benth. in Trans. Linn. Soc. 30:371. 1875.

Acacia flava Spreng. ex DC. Prodr. 2:469. 1825.
Piptadenia suaveolens Griseb. Fl. Brit. W. Ind. 710. 1864; nom. nudum, not Miq.
Piptadenia leptocarpa Rose, in Contr. U. S. Nat. Herb. 1:325. 1895.
Mimosa buceragenia B. L. Robins., in Proc. Am. Acad. 43:23. 1907, fide Britt. & Rose.

Erect to procumbent small tree or shrub, the branchlets glabrous or sparsely puberulent, inconspicuously lenticellate, often longitudinally striate or ridged, usually sparsely armed with rather small, scattered, recurved thorns. Leaves large, bipinnate, the pinnae 6–11 pairs, more or less opposite, the leaflets many (frequently 25 or more) pairs per pinna; petiole 1–4 cm. long, subterete, sulcate above, glabrous or pubescent, bearing a shallow, oblong, cupulate gland usually near the middle; rachis up to 25 cm. long, usually puberulent above, eglandular except sometimes bearing a cupulate gland at insertion of terminal pair of pinnae; pinnular rachis up to 8 cm. long, usually bearing a small gland at insertions of distal 1–2 pairs of leaflets, pubescent, subalate; leaflets linear, 4–8 mm. long and 1–2 mm. wide, broadly acute apically, asymmetrically rounded or truncate basally, glabrous, the costa excentric baseward, the secondary venation remote, ascending; stipules linear-setiform, as much as 6 mm. long. Inflorescence of elongate, pedunculate, axillary spikes, these solitary or few-fasciculate, near the tips of twigs arising from nodes not yet foliate and hence appearing somewhat paniculate; peduncles usually less than 1 cm. long, subtomentose; spike commonly about 6–7 cm. long, the axis pubescent, the flowers moderately dense, the floral bracts minute. Flowers sessile, reported yellow; calyx cupulate, about 1 mm. long, 5-lobed, glabrous; corolla of 5, free, nearly linear petals about 3 mm. long, glabrous; stamens normally 10, free, inserted atop a short tube or androgynophore, 5–6 mm. long; anthers broadly oblong, almost 1 mm. long, bearing an apical gland, glabrous; ovary glabrous, conspicuously stipitate, apparently abortive in some flowers; stigma narrow. Legume broadly linear, 5–9 cm. long and about 15 mm. wide, thin, glabrous, glandular when young, the surface irregular because of maturing seeds but not constricted between the seeds.

Mexico to northern and western South America.

Coclé: Aguadulce, *Pittier 4890*.

Vegetatively (or even in fruit) *P. flava* resembles species of *Leucaena* and *Acacia*. The elongate spike, however, tends to distinguish it from similar species of these other genera in Panama. *P. viridiflora* and/or *P. communis* may with comprehensive study prove to be synonyms of this species.

15. ENTADA Adans.

ENTADA Adans. Fam. Pl. 2:318. 1763, nom. conserv.

Gigalobium P. Br. Nat. Hist. Jamaica, 362. 1756.
Perima Raf. Sylva Tellur. 118. 1838.
Strepsilobus Raf. loc. cit. 117. 1838.
Adenopodia Presl, Epim. Bot. 206. 1850, fide Hook. Jour. Bot. 4:286. 1852.
Pusaetha [L. 1747] Ktze. Rev. Gen. Pl. 1:204. 1891.
Entadopsis Britt., in N. Am. Fl. 23:191. 1928.
Pseudoentada Britt. & Rose, loc. cit. 1928.

Woody vines or climbing shrubs or trees, usually very large, unarmed (in Panama) or aculeate, sometimes cirrhiferous. Leaves large, bipinnate, the pinnae few pairs (in Panama) or less frequently several to many, opposite, the leaflets few to many pairs; petiole and usually the rachis eglandular, the rachis sometimes terminating in a bifurcate tendril; leaflets large or small; stipules small. Inflorescence of usually elongate spikes, these solitary and borne from foliate branches or clustered terminally in a large raceme; floral bracts minute. Flowers small, usually briefly stipitate, 5-parted, valvate, variously colored, often with a disagreeable odor; calyx small, synsepalous, broadly and shallowly cupulate; corolla of 5 free or slightly coherent petals; stamens 10, free, briefly exserted; anthers tipped with a (caducous) gland; ovary several- to many-ovulate; style slender; stigma terminal, truncate. Legume often very large (Panamanian species), flat, straight or curved, the valves in time breaking into segments, the margins continuous and persistent.

At least one species pantropical; others chiefly African and tropical American.

A comparatively small genus of less than 20 species, many of which are dissimilar to the others and a cause for past generic segregation. It seems scarcely advisable, however, to accept division of *Entada* into several smaller genera based on these differing species, for such a procedure, if followed generally here and in the MIMOSOIDEAE as a whole, could continue *ad infinitum* until practically no "genus" could be readily located. The Panamanian species of *Entada* suggest, at least superficially, giant liana-type Mimosas, but can be readily distinguished by the long spikes of flowers which are not found in any of the Panamanian species of *Mimosa*. The leaves are sometimes reported sensitive, folding following disturbance, such as is the case with a number of *Mimosa* species. Two species of *Entada* are known to occur in Panama, both distinctive vines of lowland areas.

a. Inflorescence a supra-axillary spike; leaves often cirrhiferous; legume very large, the seed 3–5 cm. in diameter..... 1. E. GIGAS
aa. Inflorescence a terminal raceme of spikes; leaves seldom with tendrils; legume smaller, the seeds only about 1 cm. long..... 2. E. POLYSTACHYA

1. ENTADA GIGAS (L.) Fawc. & Rendle, Fl. Jamaica 4:124. 1920.

Mimosa gigas L. Fl. Jam. 22. 1759.
Entada gigalobium DC. Prodr. 2:424. 1825.

Large vine of lowland areas, often climbing to the tops of forest trees, the branchlets essentially glabrous and inconspicuously lenticellate. Leaves very large, bipinnate, commonly cirrhiferous, the pinnae usually 2 pairs, opposite, the leaflets

3–6 pairs per pinna; petiole usually 2–4 cm. long, eglandular, frequently puberulent, callous basally; rachis similar to the petiole, up to 20 cm. long, eglandular, commonly terminating in a stout, branched tendril, especially on new growth; pinnae up to 15 cm. long, the axis similar to the rachis; leaflets asymmetrically oblong, the terminal ones as much as 8 cm. long and 3 cm. wide, the basal ones as small as 1.5 cm. wide and 1 cm. broad, usually blunt or even emarginate apically, inequilaterally obtuse basally, glabrous except on the costa, somewhat glossy above, dull below, the venation conspicuous, the secondary lateral veins essentially parallel; stipules linear, about 4 mm. long. Inflorescence an elongate spike, supra-axillary (usually inserted 5–10 mm. above the axil), the peduncular portion only 1–5 cm. long, the floriferous portion 7–25 cm. long, the floriferous bractlets squamiform. Flowers cream, odorous (often described as unpleasantly so, or with a "sickly odor"), short-stipitate; calyx shallowly cupulate, about 1 mm. deep, rather irregularly 5-lobed, glabrous; corolla of 5 narrowly elliptic petals about 3 mm. long, glabrous, free or somewhat connate basally; stamens 10, 6–7 mm. long, the anthers usually bearing a (caducous) gland; ovary glabrous. Legume very large, as much as 2 m. long (commonly several dm. long) and about 1 dm. broad, more or less oblong, curved, flat, transversely jointed but the margins continuous, glabrous, the segments 1-seeded; seeds orbicular, 3–5 cm. in diameter, flattened, blackish, glossy.

Central America, northern South America, and West Indies; west Africa.

BOCAS DEL TORO: Bocas del Toro, *Read s. n.* CANAL ZONE: Barro Colorado Island, *Standley 31264; Stevens 416.* PANAMÁ: San José Island, *Erlanson 15, 82; Johnston 600, 983.*

A tendriled vine, very remarkable for the enormous size of the legume, probably not equalled by that of any other species of the family in this hemisphere. It is the so-called "sea-bean," the shiny black seeds of which are carried long distances by ocean currents. The species is a lowland plant, frequently found near the seashore, and its wide distribution can perhaps be explained by discharge of the seeds into the ocean.

Dr. I. M. Johnston (mss.), who studied "sea-beans" intensively during the war years, shows that on the basis of the fruit *E. gigas* is quite distinct from the Old World *E. phaseoloides* (*?Mimosa Entada* L. Sp. Pl. 518. 1753, fide Merrill; *Lens phaseoloides* L. in Stickman, Herb. Amboin. 18. 1754; *Mimosa scandens* L. Sp. Pl. ed. 2, 1501. 1763; *Adenanthera scandens* (L.) Forster, Fl. Ins. Aust. Prodr. 33. 1786; *Acacia scandens* (L.) Willd. Sp. Pl. 4:1057. 1806; *Entada Pursaetha, E. monostachya,* and *E. Adenanthera* DC. Prodr. 2:424. 1825, fide Benth.; *E. Rheedii* and *E. Parrana* Spreng. Syst. 2:325. 1825; *Strepsilobus scandens* (L.) Raf. Sylva Tell. 118. 1838; *Entada scandens* (L.) Benth. in Hook. Jour. Bot. 4:332. 1841; *E. Gandu* Hoffm. ex Walp. Rep. 1:858. 1842, fide Benth.; *E. Rumphii* Scheff. in Natuurk. Tijdschr. Ned. Ind. 32:90. 1872, fide Benth.; *Gigalobium scandens* (L.) Hitchcock, in Rept. Mo. Bot. Gard. 4:82. 1893), a name heretofore applied to a group of similar species and including the American *E. gigas.*

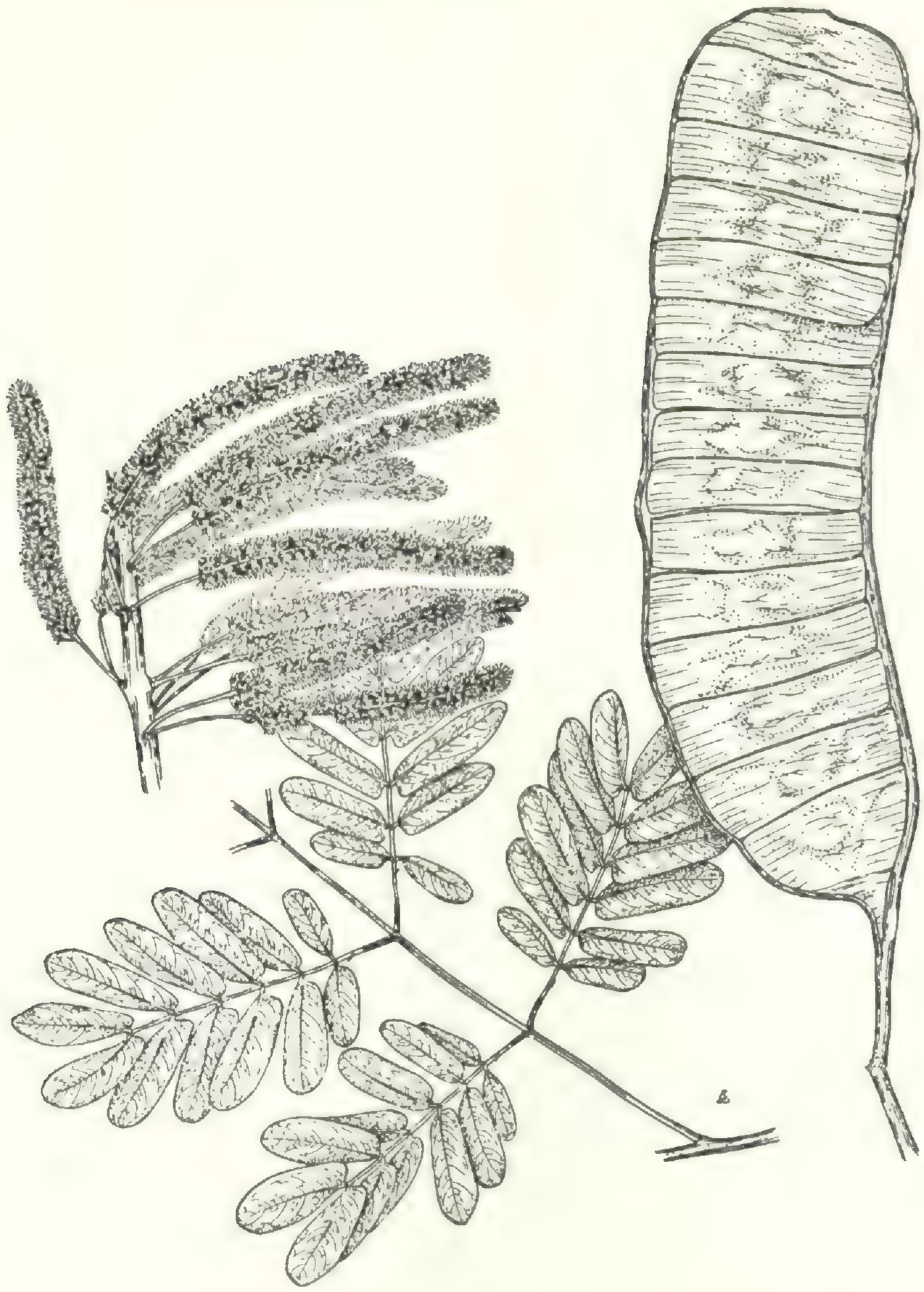

Fig. 103. *Entada polystachya*

2. ENTADA POLYSTACHYA (L.) DC. Mem. Legum. 434. 1825.

Mimosa polystochia L. Sp. Pl. 520. 1753.
Mimosa bipinnata Aubl. Pl. Guian. 2:946. 1775.
Mimosa caudata Vahl, Eclog. 3:35. 1807, fide Benth.
Mimosa chiliantha G. F. W. Mey. Prim. Fl. Esseq. 163. 1818, fide Benth.
Adenanthera Bonplandiana Kunth. in HBK. Nov. Gen. & Sp. 6:311. 1824.
Acacia caudata DC. Prodr. 2:456. 1825.
Entada Plumieri Spreng. Syst. 4^2:164. 1827.
Entadopsis polystachya Britt. in N. Am. Fl. 23:191. 1928.

Large, woody liana up to 15 or more m. tall, the branchlets glabrous, longitudinally striate, the old stems rather shaggy-barked. Leaves large, bipinnate, the pinnae commonly about 4 pair, opposite, the leaflets mostly 5–8 pairs per pinna;

petiole mostly 4–8 cm. long, eglandular, glabrous, flattened above; rachis similar to the petiole, eglandular; pinnae usually 6–15 cm. long, the axis often puberulent above; leaflets oblong, 15–40 mm. long and 5–18 mm. wide, usually rounded apically and obliquely so basally, glabrous or sometimes sparingly pubescent below or along the margins, glossy above, the venation prominently reticulate; stipules linear, small, caducous. Inflorescence a large, terminal raceme (often 2 dm. long) of slender spikes, the latter 6–7 cm. long, inserted singly or in pairs; floral bractlets not apparent; axis usually puberulent. Flowers small, very briefly stipitate, reported reddish, pinkish, whitish or greenish, with a disagreeable odor; calyx shallowly cupulate, scarcely 1 mm. deep, briefly dentate, glabrous; corolla of 5, free, narrowly oblong, glabrous petals about 2 mm. long; stamens 10, somewhat exceeding the petals, glabrous, the anthers (at least in youth) gland-tipped; ovary glabrous. Legume large, oblong, commonly 25–30 cm. long and 6 or 7 cm. wide, curved, flat, thin, glabrous, lustrous, the valves in time breaking into segments, the margins persistent; seeds comparatively small, oblong, no more than 1 cm. long.

Mexico to middle South America; West Indies.

BOCAS DEL TORO: Chiriquí Lagoon, *H. von Wedel 1062, 1214, 2495, 2743.* CANAL ZONE: Frijoles, *Bro. Heriberto 113;* Miraflores Lake, *P. White 256.* HERRERA: Pese, *Allen 804.* PANAMÁ: R. La Maestra, *Allen 34;* Juan Díaz, *Standley 30518.*

The species is an interesting tall vine of the lowland areas, with a large, terminal, disagreeably odoriferous inflorescence and large, persistent legumes. Macerated root or stem reportedly produces a soap-like lather with water, suitable for washing.

16. PENTACLETHRA Benth.

PENTACLETHRA Benth. in Hook. Jour. Bot. 2:127. 1840.

Trees, the branchlets coarse, the leaves few-ranked. Leaves very large, bipinnate, the pinnae many pairs, opposite, the leaflets many pairs per pinna; petiole and rachis eglandular; leaflets small, numerous, inequilateral or falcate; stipules small. Inflorescence of stout, elongate spikes, apparently ebracteate. Flowers moderately small, 5-parted, rather coriaceous; calyx cupulate, the rounded lobes somewhat imbricate in bud; corolla of 5 petals connate below the middle, valvate; stamens 5, exserted, united below (with staminodia) into a very short tube; staminodia 5 (in Panama), 10 or 15, usually about 3 times as long as the stamens; anthers relatively large, gland-tipped; ovary subsessile, the stigma expanded, terminal. Legume large, flat, thick, woody, broadest above the middle, elastically 2-valvate, longitudinally striate.

Tropical America; Africa.

The genus consists of a single New World and one or two African species. It is allied to *Parkia* (South American and Old World), but the latter has a short or subcapitate inflorescence and 10 fertile stamens.

Fig. 104. *Pentaclethra macroloba*

1. PENTACLETHRA MACROLOBA (Willd.) Ktze. Rev. Gen. Pl. 1:201. 1891.

Acacia macroloba Willd. Sp. Pl. 4:1060. 1806.
Mimosa macroloba Poir. in Lam. Encycl. Meth. Suppl. 1:66. 1810.
Acacia aspidioides G. F. W. Mey. Prim. Fl. Esseq. 165. 1818, fide Benth.
Pentaclethra filamentosa Benth. in Hook. Jour. Bot. 2:127. 1840.
Pentaclethra brevipila Benth. loc. cit. 128. 1840, fide Benth.
Caillea macrostachya Steud. in Flora 26:759. 1843.
Entada Wrbeana Presl, Epim. Bot. 206. 1850, ex char. fide Benth.

Unarmed tree, the branchlets stout, longitudinally striate, puberulent when young, callous in age. Leaves very large, bipinnate, the pinnae many (usually 15–20) pairs, opposite, the leaflets many pairs per pinna; petiole 1–5 cm. long, eglandular, terete except shallowly sulcate above, callous basally; rachis as much as 3 dm. long, pubescent above, eglandular; pinnae 2–10 cm. long, eglandular;

leaflets small, linear-subfalcate, mostly 6–9 mm. long and 1–2 mm. wide, sharply acute-acuminate apically, obliquely rounded or truncate and more or less auriculate on the proximal side basally, essentially glabrous, darker and lustrous above, the venation fairly prominent below; stipules small, linear. Inflorescence of few or several terminal and subterminal, elongate spikes; peduncular portion of spike 1–5 cm. long, pubescent; floriferous portion usually 15 or more cm. long at maturity, pubescent, ebracteate. Flowers dense, sessile, 5-parted, white; calyx cupulate, 1–2 mm. long, the broad, rounded lobes shorter than the tube and somewhat imbricate in bud; petals linear-elliptic, about 5 mm. long, usually coherent for about the lower third or half of their length, glabrous, valvate; stamens 5, 6–7 mm. long, alternating with 5 thin, elongate staminodia about 2 cm. long, stamens and staminodia briefly united at the base; anthers about 1 mm. long, bearing a prominent apical gland or appendage; ovary subsessile, pubescent; style slightly exceeding the stamens; stigma expanded. Legume linear-subspatulate, 2–3 dm. long and up to 4 cm. wide, flattened but thick, ligneous, narrowed baseward, lustrous, glabrous, longitudinally striate, 2-valvate, the valves coiling backwards after dehiscence.

Southern Central America, West Indies, north-central South America.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 126;* Guabito, *Skutch 11.* DARIÉN: El Real, *Pittier 6700;* Pinogana, *Allen 935.*

A species quite different from other MIMOSOIDEAE in Panama, apparently confined to the lowlands. The large spikes of white flowers and the unusual legume make *P. macroloba* quite striking.

(Leguminosae to be concluded in Part V, Fasc. 3)

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The American Species of *Triumfetta* L. . . . . Ko Ko Lay 315–395
Miscellanea Taxonomica. I 397–408
Some American Carboniferous Fern Fructifications . . . . . .
. . . . . Sergius H. Mamay 409–476

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Annals
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Vol. 37 SEPTEMBER, 1950 No. 3

THE AMERICAN SPECIES OF *TRIUMFETTA* L.[1]

KO KO LAY[2]

Introduction

The genus *Triumfetta,* one of the largest of the Tiliaceae, is pantropic in its distribution; the total number of valid species in the genus may approximate 150 or more. Species are especially abundant in Latin America, but extend from tropical Florida through the West Indies, Mexico, and Central America, southward to Argentina.

The western-hemisphere species of the genus have received no special attention from systematists. K. Schumann's[3] treatment of the South American species, though still a standard reference, is however pathetically out of date. Standley's[4] classification of the Mexican species is generally more acceptable, but an array of new species has been established since his publication. About 150 species have been named for this hemisphere, and it was thought desirable to monograph the genus for the New World in order to establish the proper status of the species.

It is realized that the present splitting of the genus with regard to its occurrence in the eastern and western hemispheres, though convenient, is definitely not natural. At least three species which are represented in Latin America are also known to occur in the eastern hemisphere. There is a possibility that other species may have similar distribution. Since this study was undertaken with a view to clarify the species of the western hemisphere, the total range and the remaining species of the genus have of necessity been ignored.

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[1] An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Washington University.

[2] Lecturer in Botany, University of Rangoon, Burma. Formerly Burma State Scholar in the Henry Shaw School of Botany of Washington University.

[3] K. Schumann, in Mart. Fl. Bras. 12^3:131. 1886.

[4] Standley, in Contr. U. S. Nat. Herb. 23^3:741. 1923.

Issued September 30, 1950.

A large quantity of specimens from nearly all the major herbaria of Europe and of both North and South America has been available for the study. About fifty plants of three species were also grown in a greenhouse, but the living plants were not amenable to such conditions and though they grew steadily none flowered. Hence this study is based entirely on the standard herbarium methods.

In trying to understand the morphology and to clarify the basic species concept in the genus, I realized, as with some previous systematists,[5, 6] that the characters derived from the fruits are easily ascertainable and highly constant for most species. After a primary classification of all the fruiting specimens, an attempt was made to correlate them with the flowering ones. This is rendered imperative, as it is but rarely that one finds both the fruiting and flowering materials on the same specimen. It soon became apparent that certain species are exceedingly distinct in both fruit and flower, while others show considerable variation in the floral characteristics. The species that show the greatest diversity in floral characters are also found to possess extremely polymorphic leaves. To this category belongs the *semitriloba* complex, wherein the greatest number of species have been named.

Mass collections, kindly placed at my disposal by Dr. Edgar Anderson, were studied for two species: *T. semitriloba* and *T. Calderoni.* Though no conclusive proof was arrived at, the study gave sufficient indication that introgression between the species is rampant. The species *T. semitriloba* tends to approach *T. Lappula,* on the one hand, in its characteristic, more or less pandurate leaves and very condensed nodose cymes by the foreshortening of the peduncles and pedicels; and, on the other, *T. bogotensis* by its larger flowers, more showy petals, more densely pubescent fruits, and also by the presence of short simple hairs on the leaves. The variation in the types of inflorescences, and especially the abortion of spines on the surfaces of the fruits (with their presence only on the lateral margins), tend to merge *T. Calderoni* with the genus *Heliocarpus.* Were it not for the presence of the urceolus, certain specimens of *T. Calderoni* would definitely break the generic separation between *Heliocarpus* and *Triumfetta.*

Despite the great quantity of material available for study, at least a third of the species are very imperfectly known; six species being represented only by the types. The genus further presents a problem in distribution, a great many species being strict endemics while a few are pantropic weeds.

A number of species of widespread distribution, as *T. semitriloba, T. bogotensis, T. Bartramia* and others, apparently have an infinite capacity for variation in minor characters of leaf size, shape, and indument. The extremes often seem quite distinct in themselves but in a study of large numbers of collections they appear to lose their seeming significance. Wherever such intergradations have been found, I have reduced a number of previously described species to synonymy. At the same time I have described a number of novelties which in my opinion are new to

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[5] Masters in Oliver, Fl. Trop. Africa 1:254. 1868.
[6] Sprague & Hutchinson, in Jour. Linn. Soc. Bot. 39:231. 1909.

science. With greater abundance of material in the future and intensive study of the genus further reduction may be in order.

History

The genus *Triumfetta* was proposed by Plumier[7] in 1703, in honor of John Baptiste Triumfetti of Bologne, doctor in medicine, lecturer in botany, and director of the botanical garden at Rome. Linneaus[8] in 1737 adopted the genus and described both calyx and corolla, which were depicted in Plumier's rough illustration. In the same year Linneaus[9] gave a detailed description under the same generic name of a plant growing in Clifford's garden, received from either Jamaica or Bermuda, and described it as apetalous. In 1742[10] he altered the description of the genus and stated that it lacked the calyx (corolla). In the first edition of 'Species Plantarum',[11] the description in 'Hortius Cliffortianus' was cited for *T. Lappula*, the only species named under the genus.

Linneaus had already established the genus *Bartramia*[12] which, according to Fawcett and Rendle, was based on a plant in Hermann's Herbarium (now in Herb. Mus. Brit.) with both calyx and corolla. The species *Bartramia indica* was published in 'Species Plantarum' on an earlier page (p. 389) than *Triumfetta Lappula*. As synonyms under *B. indica* Linneaus cited, among others, one of Plukenet's[13] drawings which is rather aptly done and quite diagnostic. Six years later, Linneaus[14] included *Bartramia* in *Triumfetta* and altered the trivial by naming the species *T. Bartramia*.

De Candolle[15], being unable to determine the identity of *T. Bartramia* on the ground that the synonyms cited include many diverse species, adopted Jacquin's name *T. rhomboidea.*[16]. Later botanists followed De Candolle till recently when Fawcett and Rendle[17] established that *T. Bartramia* and *T. rhomboidea* are conspecific. It is, however, to be noted that the earliest trivial is *indica*, but as Lamarck[18] subsequently described *T. indica*, the identity of which is doubtful, it is desirable to adopt the Linnean name *T. Bartramia*. Gaertner[19] maintained the two genera as distinct and further distinguished them by the presence of indivisible fruit with 1-seeded loculi in *Triumfetta*, and divisible fruit and 2-seeded loculi in *Bartramia*. The fruit of *T. Bartramia* is not really dehiscent, but it could be made to separate into component valves by prolonged boiling.

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[7] Nov. Pl. Amer. Gen. 40, *t. 8.* 1703.
[8] Gen. Pl. ed. 1. 344. 1737.
[9] Hort. Cliff. 210. 1737.
[10] Gen. Pl. ed. 2. 243. 1742.
[11] Sp. Pl. ed. 1. 444. 1753.
[12] Fl. Zeylanica, 77. 1748.
[13] Almagest. Bot. 206, *t. 41, f. 5.* 1691.
[14] Syst. Pl. ed. 10. 1044. 1759.
[15] Prod. 1:508. 1824.
[16] Enum. Pl. Carib. 22. 1760.
[17] Jour. Bot. 59:224. 1921.
[18] Encyc. Meth. 3:420. 1789.
[19] Fruct. & Sem. 2:137. 1791.

De Candolle[20] finally united the two genera and established two sections Bartramia and Lappula based on Gaertner's diagnosis, where Lappula is separated from Bartramia by the lack of petals and by its indivisible fruits. Endlicher[21] adopted the sections of De Candolle but defined them entirely on the fruit characters. Baillon[22] substituted the name Eutriumfetta for Lappula and still distinguished it from Bartramia by the indehiscent fruit. K. Schumann[23] was dissatisfied with the classification based entirely on the characters of the fruit. To him the fruits (and also the leaves) were extremely polymorphic and did not offer any constant characters. He redefined the sections, basing his classification entirely on floral characters: Eutriumfetta being apetalous and without a glandular gonophore, and Bartramia with manifest petals and glandular gonophore.

Sprague and Hutchinson[24] disagreed with K. Schumann's classification as it separated the two very closely related species *T. semitriloba* and *T. Lappula*. They in turn proposed a new classification based on a study of fruits, inflorescences and certain characters derived from the indument of the sepals. According to them, the genus is divided into the following four sections:

1. Lepidocalyx: Calyx scaly without; stamens numerous (25–60); ovary 10-loculate, each cell with 1 ovule; fruit spheroid, woody, 8- to 10-loculate, each 1-seeded, the spines fusiform.
2. Propa: Calyx not scaly; stamens numerous (25–40); ovary 6- to 10-loculate, each with 1 ovule; fruit spheroid, woody, 6- to 10-loculate, each 1-seeded, the spines constricted at the base and the tip.
3. Lasiothrix: Calyx not scaly; stamens usually numerous (20–50), rarely few; fruit spheroid, not woody, very light, indehiscent, often 1-seeded, the spines weak, with plumose tip.
4. Lappula: Calyx not scaly; stamens numerous or few; fruit spheroid or ovoid, dehiscent or indehiscent, many- or 1-seeded, the spines rigid, the tips rarely plumose.

Since the above classification, there has been no appreciable study of the genus as a whole. Hochreutiner's[25] work is more in the nature of reorganization of the tribe Grewieae than of the genus itself.

Geography

Triumfetta is pantropic in its distribution. There are 43 species in the western hemisphere, about 50 in Africa and 10 in Australia. The number of valid species in Asia is not known, but may approximate 40 or more. *T. Bartramia* and *T. Lappula* are equally at home in both the eastern and western hemispheres. *T. semitriloba* is abundantly represented in the western hemisphere and to a lesser

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[20] Loc. cit. 506. 1824.
[21] Gen. Pl. 1008. 1840.
[22] Hist. Pl. 4:195. 1873.
[23] Mart. Fl. Bras. 12^3:131. 1886.
[24] Jour. Linn. Soc. Bot. 39:233. 1909.
[25] Ann. Conserv. Jard. Bot. Genève 18:92. 1914.

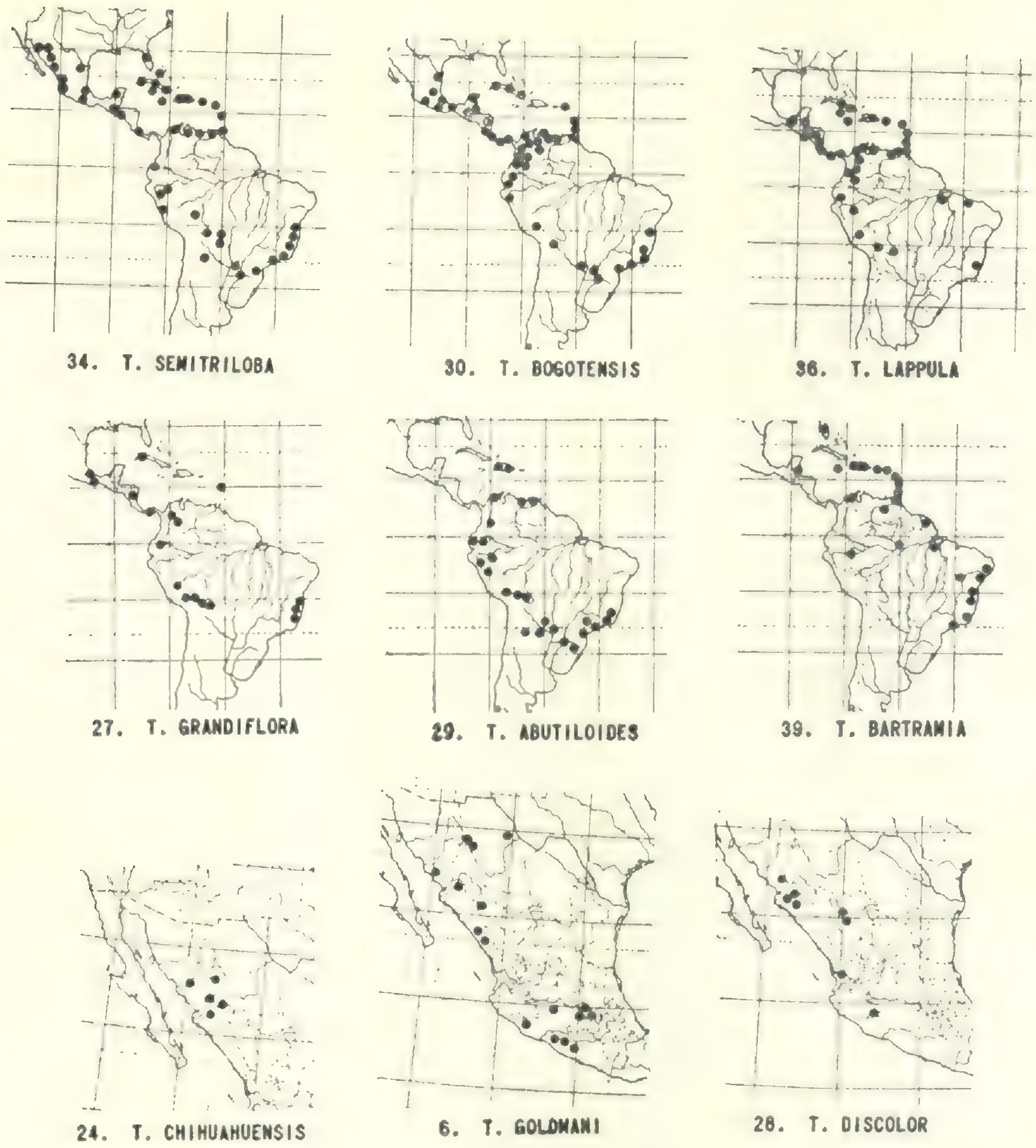


Fig. 1. Geographical distribution of species of *Triumfetta*.

extent in Africa and eastern and southeastern Asia. In the western hemisphere the species extend from tropical Florida to the West Indies, Mexico, and Central America southward to northern Argentina. Species are especially abundant in Mexico and Central America.

There are six species with very extended ranges found in both North and South Americas. The three very closely related species, *T. bogotensis*, *T. semitriloba*, and *T. Lappula*, have very similar ranges, each extending from Mexico and the West Indies through Central America southward to northwestern South America, finally to central and eastern South America. *T. grandiflora*, one of the more primitive species, has similar north-south distribution, but is rather sparsely represented throughout its range. *T. Bartramia*, whose affinities with the western-hemisphere species is rather doubtful, has an altogether distinct distribution. It

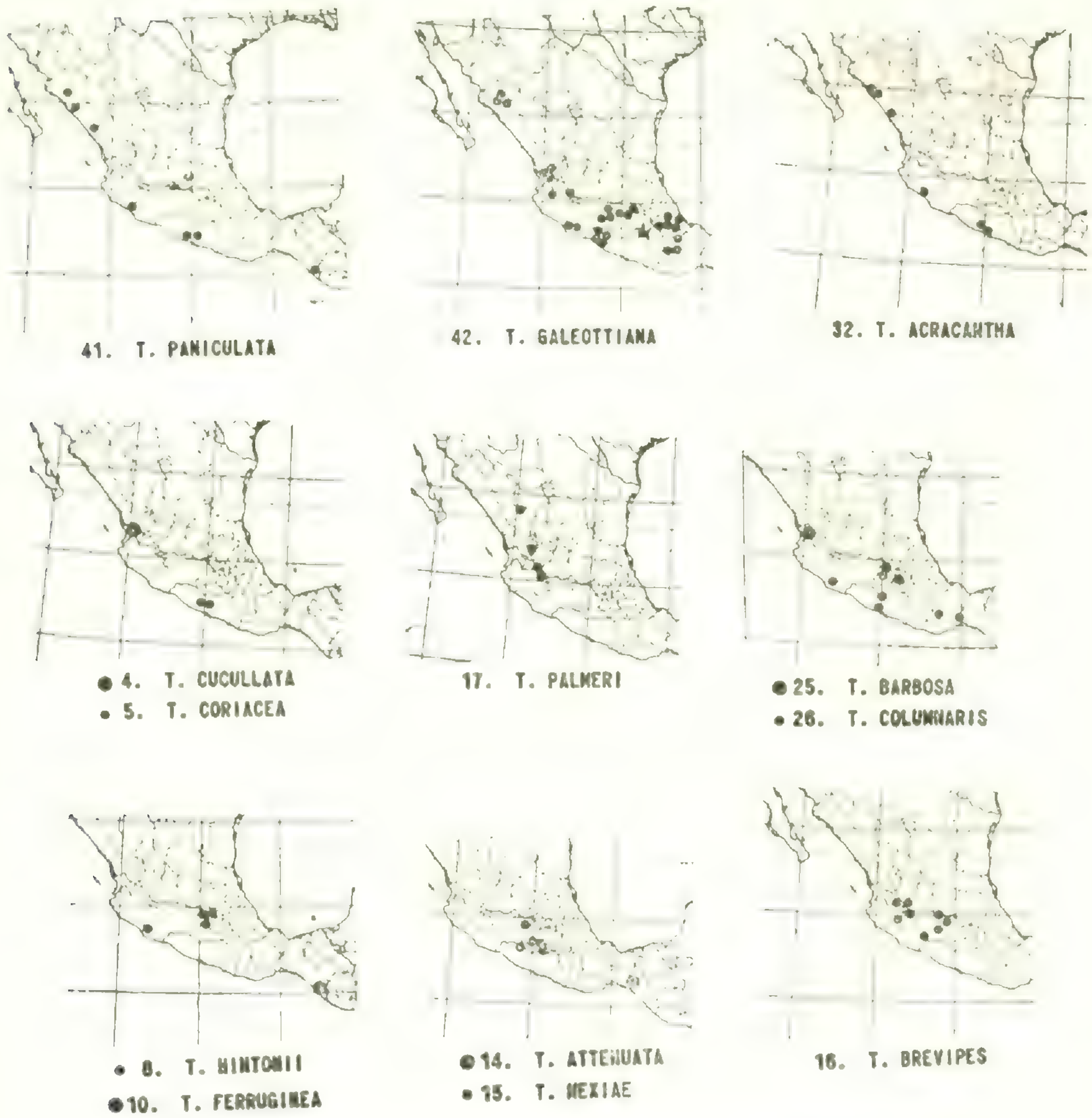


Fig. 2. Geographical distribution of species of *Triumfetta*.

is known in the West Indies and eastern South America, and except for one locality in British Honduras and in Florida, where introduced, it is not represented on continental North America. *T. abutiloides* approximates the distribution of its closely allied species *T. bogotensis*, except that it is not known in continental North America.

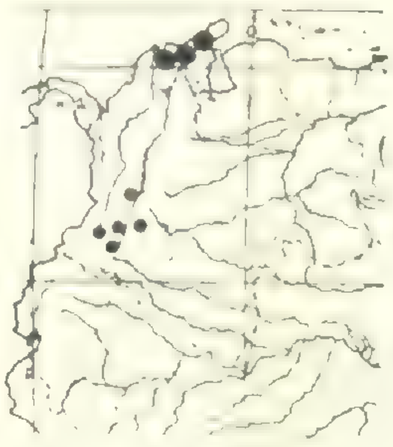
There are nine species known only from South America. *T. althaeoides*, which frequents lowland sandy areas, is austral in its distribution, and is found extensively in northern South America wherever suitable habitat is available. *T. obscura*, which is the counterpart of *T. acracantha* from Mexico, is confined to southeastern Brazil. *T. Sampaioi*, a species closely related to *T. Bartramia*, is known only in the lowlands of northeastern Brazil. The three closely related species, *T. longicoma*, *T. multilocularis*, and *T. mollissima*, are found exclusively in southeastern Brazil, Peru, and Colombia respectively. *T. caudata*, *T. sericata*, and *T. persimilis* occupy narrow ranges in Colombia.

● 1. T. STELLATA
• 2. T. POLYANDRA

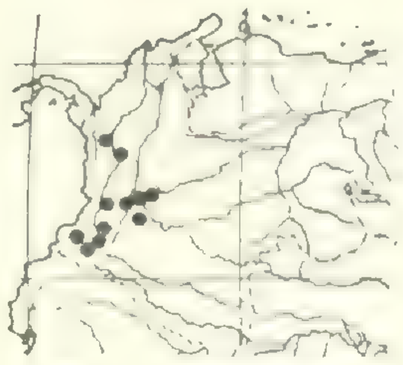
3. T. SPECIOSA

• 9. T. CALDERONI
●11. T. ARBORESCENS

33. T. ALTHAEOIDES

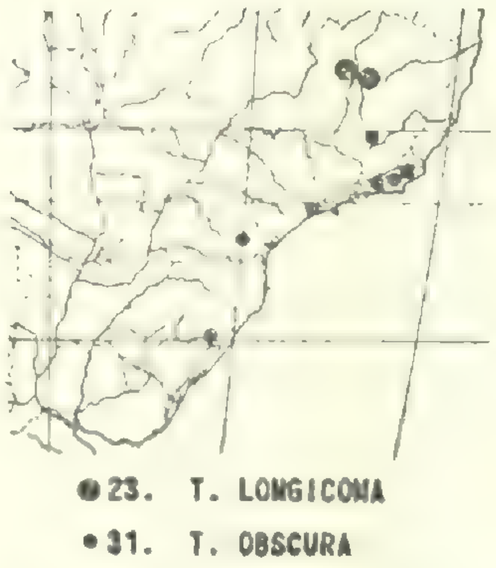


● 7. T. CAUDATA
•37. T. SERICATA

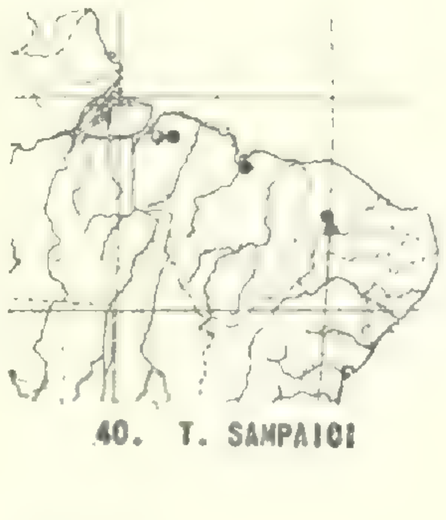


22. T. MOLLISSIMA

21. T. MULTILOCULARIS



● 23. T. LONGICONA
• 31. T. OBSCURA



40. T. SAMPAIOI

Fig. 3. Geographical distribution of species of *Triumfetta*.

The majority of the species are found in Mexico, and among them are a few that extend into Central America. The two more primitive species, *T. polyandra* and *T. speciosa*, though found sparsely in any particular locality, extend southward into Central America. Most of the species are known only from central and western Mexico. *T. discolor*, *T. Goldmani*, *T. acracantha*, *T. paniculata*, and *T. Galeottiana* are the most prominent species of western Mexico, while *T. brevipes*, *T. Palmeri*, and *T. columnaris* are found rather abundantly in central and southwestern Mexico. The rest of the species are endemics, being known from very restricted areas.

The series GENICULATAE is best represented in Mexico and Central America. Of its fifteen species only two (*T. caudata* and *T. persimilis*) are from Colombia. Because of the presence of the majority of species in central Mexico and northern Central America, including most of the primitive ones and also many very restricted endemics, it is assumed that the primary centre of dispersal of the species is probably from that area.

MORPHOLOGY

The species of *Triumfetta* are a diverse group of woody plants, usually small trees or shrubs. The series GENICULATAE constitutes species wherein the tree habit is most predominant, although no tree in the genus is known to exceed 5 m.

The stems are terete in all the species except *T. paniculata* where they are ridged or irregularly angled, the ridging occurring as a result of decurrent petiole bases. Certain plants, especially those in the *semitriloba* complex, have a short branch at almost every node of the main axes, while others (as represented by *T. Calderoni*) are sparsely, if ever, branched. The bark is prominently lenticellate, with either small white or large brown lenticels.

The leaves are petiolate. The length of the petiole is usually correlated with the shape of the lamina, the broadly ovate leaves being long-petiolate while the large elliptic ones are shortly so. *T. obscura* is an exception as it has elliptical leaves which are long-petiolate.

The lobing of the leaf generally is a good primary character in certain species, but in others, such as *T. semitriloba*, *T. bogotensis*, and *T. Bartramia*, the general leaf-shape is so variable that it is relatively useless as a definitive character. In general, weedy species of the genus have variously indented or lobed leaves and show much greater variation than the non-weedy ones. The margin is serrated, the serrations usually being very irregular. Most species have small glands on the basal serrations from which the mucilaginous sap exudes. In three species, *T. althaeoides*, *T. cucullata*, and *T. coriacea*, these glands are found on the petioles at the basal sinus. Because of their extreme constancy they offer an easy means of identifying these species.

The term "bract" has been used in this paper to mean the terminal leaves of a branch which subtend the cymes. The bracts are usually very prominent in plants with axillary inflorescences. They are invariably smaller and more shortly petioled than the vegetative leaves and are generally elliptical in outline. No measurements of the bracts are given, as it is difficult to determine from dried material whether they have attained their maximum growth or not.

All species have more or less coarsely pubescent leaves, except *T. acracantha* and *T. obscura* which have glabrescent ones. The leaves usually possess three tiers of induments, two of which consist of stellate hairs, one closely appressed to the surface and the other usually much larger and spreading irregularly, the third tier of simple hairs which are usually much longer and generally more prominent. The nature of the indument offers good primary characters in certain species. However, the use of this character requires great judgment as the pubescence changes considerably during the course of development. Young leaves may be covered rather densely with both stellate and simple hairs, while the mature ones on the same plant may have hairs of one kind only.

The leaves are stipulate. The stipules are usually large and linear and tend to dry from the tip to the base. They are rarely caducous; in most species they

persist even after the shedding of the leaves. No diagnostic importance has been attached to the stipules.

The inflorescence consists of compound aggregate dichasia. In the more primitive species, the cymes, each consisting of 1–3 cymules, are borne in the axils of the bracts. In the more advanced species the cymes are terminal and consist of a shortened sympodial branch system, each bearing 4–6 cymules. There is usually more than one cyme per bract, the cymes being clustered rather densely at the nodes, and the whole inflorescence is usually large and spreading. In both types of inflorescences the cymule is either 2- or 3-flowered. Each cymule is subtended by a pair of fugacious bracteoles. The number of flowers per cymule is not constant even on the same inflorescence, probably due to the abortion of one of the lateral flowers in early ontogeny. The inflorescences are hermaphrodite or, in a few species, gynodioecious.

The species of the genus have considerable range in the size of flowers. Slightly before anthesis the floral buds of *T. polyandra* and *T. speciosa* are as large as 3–4 cm. in length, while those of *T. Lappula* and *T. heliocarpoides* rarely, if ever, exceed 6 mm. The size of the flower is generally a good constant character for most species. However, in *T. bogotensis* the length varies from 7 to 13 mm. and is not correlated with the variations in either the fruit or vegetative characters.

The floral buds in the majority of the species are oblongoid, but in the *Galeottiana* and *Calderoni* complexes they are obovoid in the hermaphrodite flowers.

The sepals afford good specific characters. All plants of the genus bear a subapical appendage on the sepals, the lengths of which are generally constant for a given species. *T. Purpusii* and *T. falcifera* possess the longest appendages, usually about 5 to 7 mm. long, and *T. Calderoni* the shortest, being nearly obsolete. Unless otherwise mentioned, the lengths of the sepals given in this paper include the apical appendages. The indument of the sepals may also be used as a primary character in certain species. However, as with the pubescence of the leaves, its use in the identification of a species needs caution.

There is a tendency in the genus towards a completely apetalous condition. The more primitive species, such as *T. polyandra, T. multilocularis, T. brevipes* and others, have large showy petals, while the more advanced species *(T. Lappula, T. Galeottiana,* and *T. heliocarpoides)* are either apetalous or possess very small ones. The petals have a short ciliate claw, which is hairy on the outside and sometimes has a transverse band of stellate hairs on the inner surface at the base of the blade.

The androgynophore or gonophore, with its five spherical or elliptical glands, contributes some important diagnostic characters. The shape of the glands, their size, and whether they are contiguous or otherwise, are usually constant for a species. Because of their extreme smallness, these characters, though mentioned in the specific descriptions, have not been used in the key. The gonophore is slightly accrescent in fruit. *T. Lappula* is the only species known which does not possess a glandular gonophore.

The urceolus is a small, rather membranaceous ring with a ciliate margin, which is borne on the gynophore and completely surrounds the base of the stamens. It is usually 5-lobed, sometimes 10-lobed, and very rarely unlobed. *T. Lappula* and *T. Sampaioi* do not possess an urceolus.

The stamens are borne cyclically on the gonophore, and the number is of great importance in specific criteria. Certain species have as high as 60 *(T. attenuata, T. arborescens)*, others have about 40 *(T. polyandra, T. Purpusii, T. paniculata)*, while the majority of the species possess between 15 and 25. *T. Sampaioi* is the only species in the western hemisphere which has only 5 stamens. The smaller numbers are rather rare in *Triumfetta.* At least three species are known to be gynodioecious. In these the pistillate flower either has staminodes or lacks them completely. No staminate flower is known for the whole genus.

The filaments have retrorse serrations in both the *semitriloba* and *Bartramia* complexes. Other species have smooth filaments. In *T. chihuahuensis* the bases of the filaments are lightly stellate-pubescent. The anthers do not yield any character of diagnostic value. They are always dorsi-fixed, consisting of two thecae, each with two introrse, longitudinally dehiscing cells. The pollen grains are ellipsoidal, and about 50 μ long and 35 μ wide. The surface is minutely rugulose to very nearly smooth.

The number of cells of the ovary is a good specific character. In the series Geniculatae, the ovary is invariably 2-merous, and in most species of Uncinatae it is 3-, and rarely 2-loculate. Where the ovary is too small for convenient dissection, the number of locules may be ascertained by dissecting a very small floral bud, and counting the number of stigma lobes. In more mature buds the stigmas, in most species, fuse and do not separate easily. In certain species, however, the stigmas remain separate throughout. The descriptions of the stigma under each species in this paper is that of the later stage.

The style is usually much longer than the stamens, and the stigma is generally exserted above the anthers. However in *T. dioica* and the species of the *Galeottiana* complex the style is shorter than the stamens and the stigma is included by the anthers. It may be of interest to note that these species are the only ones known in the genus which exhibit gynodioecism.

The spinules are small transparent epidermal outgrowths of the ovaries. They are the first to differentiate on the ovaries and retain their shape and size on the mature fruits. They are probably secretory in function, as there are large quantities of mucilage in the early stages of ovary differentiation. In the series Stellatae and Geniculatae these spinules are always straight-pointed, while in Uncinatae they are arcuately recurved. After fertilization, the spines develop from the pericarp, each at the base of a spinule. Sometimes, as in *T. caudata* and especially in *T. Hintonii*, spines fail to develop from every spinule. The spinules are thus carried at the tips of the spines, and usually harden slightly after anthesis. Whatever their degree of rigidity, the spinules are always transparent and hyaline. The nature of the spinules on young fruits, slightly after fertilization, is the best

criterion for determining to which series the plant belongs.

The fruit is the best single character for determining the species. The shape is generally constant for a species. *T. caudata, T. Hintonii,* and *T. socorrensis* possess oblongoid fruits, while the rest of the species have either spheroid or suborbicular ones. It may be noted that these three species possess much fewer spines than the others.

It is often difficult to speak with certainty regarding the dehiscence of the fruits. In at least three species *(T. polyandra, T. grandiflora,* and *T. discolor)* the fruits are easily dehiscent. In certain others, such as *T. semitriloba, T. multilocularis,* and *T. althaeoides,* they are quite indehiscent. In a few the fruit can be made to separate into valves by prolonged boiling, but there is no evidence that it actually dehisces in nature.

The number of cells is constant for a given species. Each cell is potentially 2-seeded, but there is a general tendency in most species to the formation of false septae and production of double the number of cells in mature fruit, each with one seed. The reverse is true in three species, *T. Hintonii, T. Bartramia,* and *T. Lappula,* where one or more cells abort early in the process of fruit development.

The size of the mature fruit body shows little variation. However, care is needed in the use of this character, as it often is difficult to know from dried material whether a fruit is mature. In general, species with large showy flowers tend to have relatively large fruits. *T. althaeoides* and *T. paniculata* are obvious exceptions as they possess rather large fruits but have very small flowers.

The nature of the pubescence on the fruit is less variable than that of the leaves and stems. Certain species, such as *T. Mexiae* and those in the *Galeottiana* complex, possess glabrous fruits. Sometimes two rather closely allied species may be essentially different only in the pubescence of the fruit body *(T. Purpusii* and *T. falcifera).* In *T. Lappula* a few fruits have been noticed to have densely pubescent bodies and long plumose hairs on the spines when either diseased or attacked by insects. This may be interpreted as traumatic reversion to an ancestral character.

While the general nature of the spinules affords characters for series, those of the spines themselves are characteristic of individual species. The spines may be glabrous or pubescent. When pubescent, they may bear many long hairs (plumose) or short rather irregularly arranged hairs (irregularly pubescent) or short hairs which are all retrorsely pointed (retrorsely pilosulose). Further, the length of the spines and the number per fruit being reasonably constant for a given species, they have been found satisfactory in primary separation of the species. Section LAPPULA is characterized by rigid spines; the only known American species with more or less flexible spines is *T. longicoma.*

The seeds are either ovoid or lenticular, and have a prominent funicular groove. There is a considerable variation in the size of the seeds among the species. Measurements of the mature seeds are given under every specific description.

GENERIC AND SUBGENERIC RELATIONSHIPS

Triumfetta is commonly referred[26] to the tribe Grewieae of the family Tiliaceae and usually is recognized by its characteristic bur-like fruits. The genus is distinct from the other genera of Grewieae except *Heliocarpus*. Some of the more important distinguishing characters between the two genera have been enumerated in my revision of the genus *Heliocarpus*.[27]

In their treatment of the African species of *Triumfetta* Sprague and Hutchinson[28] divide the genus into four sections based on the texture of the fruits, the nature of the spines and the inflorescences, and some characters derived from the indument of the sepals. According to their classification all the American species belong to section LAPPULA, under which they tentatively proposed the three series STELLATAE, GENICULATAE and UNCINATAE.

Before considering the series in detail it is desirable to summarize here the characters of the genus which have been considered primitive:

1. Arborescent habit as opposed to shrubs or annuals.

2. Dense tomentum of both stellate and simple hairs on leaves and branches, usually associated with plumose hairs on spines *versus* glabrescent condition of leaves and branches together with glabrate or retrorsely pilusolose spines.

3. Simple inflorescences consisting of 1 or 2 cymules in the axils of the bracts as compared with compound aggregate dichasia where the cymes are borne in dense nodose clusters of 12–20 flowers each.

4. Large showy flowers with many stamens, and multiloculate large fruits *versus* small flowers having few stamens with a tendency towards dioecism; also marked tendency towards reduction of floral parts such as gonophore, gland, urceolus, and petals, and the general progress towards 1-loculate, small, glabrous fruits.

The series STELLATAE is known to me from only one specimen, and I am in no position to comment on its phylogeny or relative antiquity, except to say that it is very closely related to GENICULATAE. The spinules on the ovary are straight and undivided and resemble those in GENICULATAE; but in fruit they consist of 4 to 5 per spine and are stellately arranged.

The series GENICULATAE is a relatively small group consisting of 14 species, most of which are rather poorly represented in the herbarium. The species of this series generally possess a tree habit, 2-merous ovary, usually numerous stamens, and ovaries bearing spinules which are either straight or slightly deflexed in fruit, but never recurved. Each spine is terminated by one spinule only. These characters, together with the obvious consideration that a hooked spinule of UNCINATAE is definitely more efficient in the dispersal of fruits than the straight one of GENICULATAE, lead one to the conclusion that GENICULATAE is more primitive.

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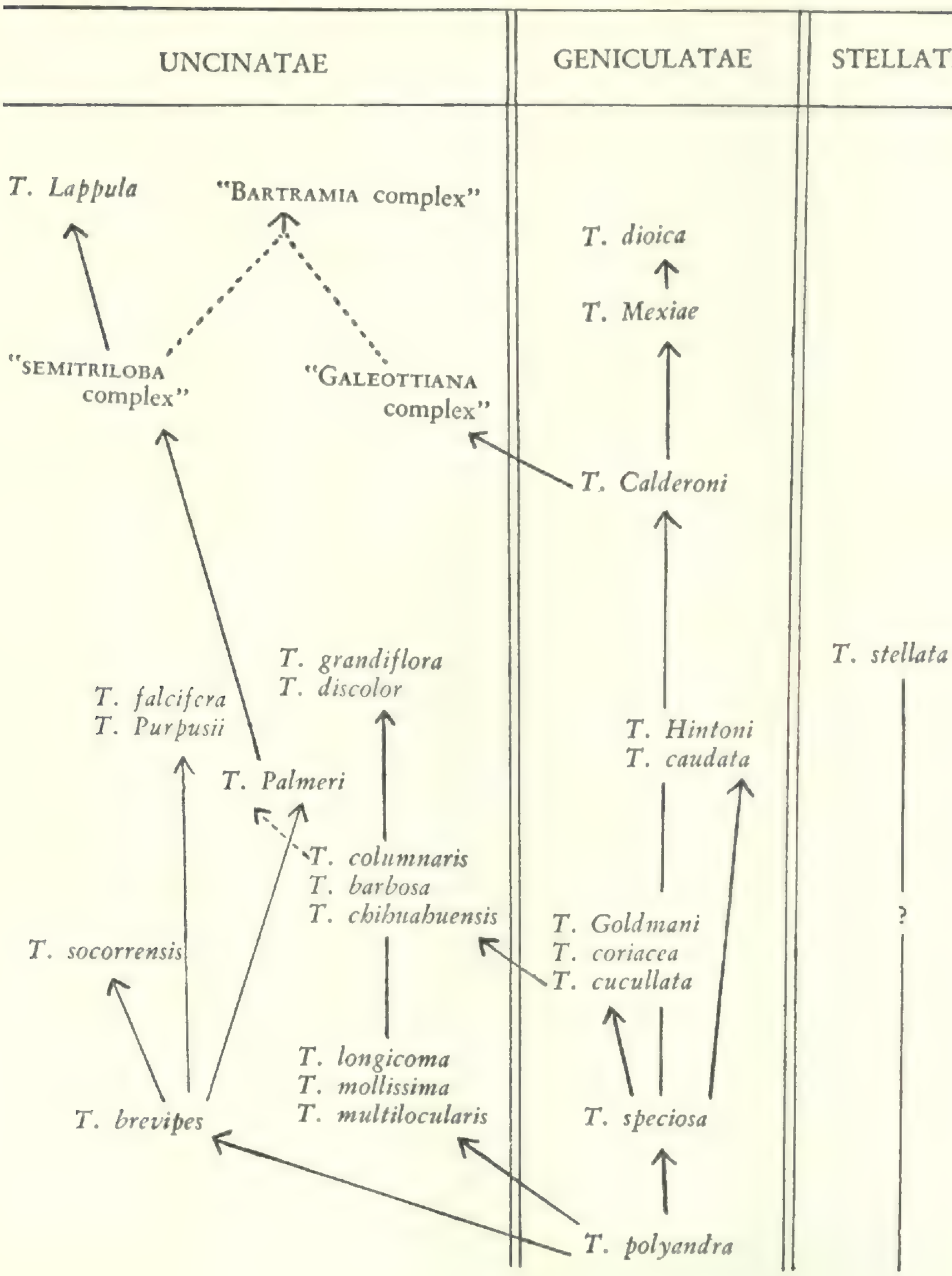
[26] K. Schumann in Engl. & Prantl, Nat. Pflanzenfam. 3^6:28. 1895.
[27] Ann. Mo. Bot. Gard. 36:508. 1949.
[28] Jour. Linn. Soc. Bot. 39:233. 1909.



Triumfetta polyandra is apparently the most primitive species of the series since it possesses very large showy flowers (the largest known for the genus), numerous stamens, and also very large fruits with very densely plumose spines. The character of the spines in turn relates it to Lasiothrix, a section considered to be more primitive than Lappula by Sprague and Hutchinson.

The derivation of the species of GENICULATAE from *T. polyandra* is apparently quite simple. *T. speciosa*, with its very large flowers and fruits and its long plumose spines, could be derived from *T. polyandra*, from which it differs in having fewer stamens and much smaller petals. By the reduction in the sizes of flowers and fruits and also in the number of spines, *T. caudata* could be conveniently arrived at from *T. speciosa*. *T. caudata* possesses very plumose spines and densely tomentose fruits, leaves, and branches. *T. Hintonii* culminates this line of reduction, as it has glabrescent leaves and branches, much smaller flowers, very few short spines, and a 1-loculate ovary due to the abortion of one locule. In *T. caudata*, and especially in *T. Hintonii*, the number of spines per fruit is usually much less than the number of spinules on the ovary.

Another line of evolution which stems from *T. speciosa* leads to the *Calderoni* complex, consisting of seven species. The more primitive species of this complex are characterized by the possession of plumose spines and small but densely tomentose fruit bodies. They all have very small flowers usually borne on compound aggregate dichasia, in which each cyme is composed of 12–20 flowers. The derivation of the flowers of this complex from *T. speciosa* is not too clear. The three species, *T. Calderoni*, *T. ferruginea*, and *T. arborescens*, are considered more primitive than the rest of the species in the complex, since they possess numerous stamens, plumose spines, and densely tomentose fruits. *T. Mexiae* is the only species of the genus which has a small gynophore borne upon the gonophore. This character, in conjunction with the glabrate fruits and spines and fewer stamens as compared with the three species mentioned above, makes *T. Mexiae* appear definitely more advanced. *T. attenuata* is very closely related to *T. Mexiae*. Dioecism is attained in *T. dioica*, a species which shows close affinity with *T. Calderoni*.

A second line of evolution from *T. polyandra* leads to *T. coriacea* and *T. cucullata*. It is unfortunate that no fruiting specimen of *T. cucullata* is available. However, in its vegetative and floral characters it is strikingly similar to *T. coriacea*, a species which has numerous stamens and large flowers with showy petals. It differs from *T. polyandra* in its smaller fruits and fewer and less pubescent spines. Except that *T. Goldmani* has fewer stamens, it has much the same characters as *T. coriacea*.

The series UNCINATAE is rather well represented in the herbarium and consists of 27 species in the western hemisphere and about 25 in the eastern. Unlike GENICULATAE, this series is not a compact group, and is apparently polyphyletic in origin, as some of the species with uncinate spinules could be derived more easily from species in GENICULATAE than from those in UNCINATAE. This series is characterized by the members having spinules which are continuously recurved both on the ovary and the spine, by their shrubby habit, by the predominance of 3-merous ovaries, and, except in the more primitive species, by the presence of only 5–25 stamens.

The most obvious direct line of evolution is from *T. brevipes* which, though advanced in many respects, could be easily referred to *T. polyandra* on such primitive characters as the size of the flowers, the presence of numerous stamens, and the large, more or less tomentose fruits with numerous though short spines. This species apparently gives rise to three lines of evolution, of which two end in strict endemism and the third attains a high degree of success and complexity.

In possessing relatively large, showy flowers, and large, more or less tomentose fruits and spines, the endemic species *T. socorrensis* is obviously related to *T. brevipes*; however, it is more advanced than the latter as the number of spines and stamens is considerably less. *T. Purpusii,* another endemic species, has the same type of fruits as *T. brevipes,* though they are slightly smaller and armed with fewer spines. Its flowers still possess numerous stamens, but are rather oddly specialized in having excessively long apical appendages of the sepals. The relationship between *T. Purpusii* and *T. falcifera* is so close that it is sometimes slightly difficult to distinguish the two species when in flower. The fruits of *T. falcifera* and *T. Purpusii* are alike in general shape and size but those of the former are nearly glabrous.

The more successful line of evolution from *T. brevipes* leads to *T. Palmeri.* An interesting specialization appears here for the first time. The spines are clothed lightly with short hairs which are all retrorsely pointed. This feature, together with hooked spinules, is of definite advantage in the dispersal of the fruits by animals. Though *T. Palmeri* has retrorsely pilosulose spines, it still possesses large flowers and fruits. The highly successful and widely distributed *semitriloba* complex may be derived from this type by the reduction in the sizes of flowers and fruits, and also by the inflorescences becoming slightly more compound. Further reductions in the floral parts leads to *T. Lappula,* a very widely distributed species of the genus.

There is a considerable confusion with regard to the delimitation of *T. semitriloba.* Some authors[29, 30] treat it in a very inclusive sense, to include all plants which have retrorse hairs on their spines but are not *T. Lappula.* This inclusive interpretation is not satisfactory, because some of the segregate species are distinct even to a casual observer.

It is more usual to split the complex into many species, chiefly distinguishing them on the size of the flowers, shape and size of the leaves, and on pubescence. This treatment does not solve the problem either, as most of the so-called species appear to be connected by numerous intermediate forms which defy classification in the herbarium. The difficulty is further enhanced by the incomplete nature of the specimens, classification being frequently uncertain in the absence of mature fruit.

The variation in the size and shape of the leaves is of such great magnitude that it is usually impossible to match two specimens with any degree of certainty by

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[29] K. Schumann in Mart. Fl. Bras. 12^3:135. 1886.
[30] Uittien in Pulle, Fl. Surinam 3:56. 1932.

the use of leaf characters only. Other characters being very similar, the leaves usually may vary from undivided to deeply and profoundly 3-lobed, the lobing being either above or below the middle of the lamina. The size of the flowers is relatively less variable, but there are instances, especially in *T. bogotensis*, where it does not correlate with the other trends. The nature of the pubescence is slightly more constant, though there is a very considerable variation in the degree. Apparently the kind of hairs, whether stellate, simple, or both, is generally constant for a species, as it tends to vary with the general shape and size of the petals and fruits together with the number of locules and the nature of the spines.

On some of these more constant characters, I have recognized six species in the *semitriloba* complex, with the hope that it would be more satisfactory from both the practical and taxonomic standpoints. Some of the more important characters which help in the identification of the species are discussed briefly under each, besides those mentioned in the key.

The three South American species, *T. multilocularis*, *T. mollissima*, and *T. longicoma*, are related in but a superficial way to *T. brevipes*. The very definitely 2-merous ovaries, the general tendency towards a tree habit, and the large fruits with very plumose spines relate them more closely with *T. polyandra*. Among themselves, the relationships to one another are extremely strong. *T. multilocularis*, though a very distinct species, has hitherto been mistaken for *T. mollissima* in the herbarium. *T. longicoma* is the most advanced member of the three.

Triumfetta chihuahuensis, *T. barbosa*, and *T. columnaris* are three distinct but very closely related species. Although they have a few characters in common with *T. Palmeri*, they do not exhibit any close affinity to that species and are much more closely related to *T. coriacea* and *T. Goldmani*. Without the uncinate spinule, one would certainly experience difficulty in identifying *T. columnaris* and *T. Goldmani*. It is most probable that these three species of Uncinatae are derived directly from the three geniculate species, *T. cucullata*, *T. coriacea*, and *T. Goldmani*. *T. grandiflora* and *T. discolor* are definitely related in having dehiscent fruits and rather large showy flowers with about 20 stamens. They are in turn related to *T. mollissima*.

The *Galeottiana* complex (consisting of the three species, *T. paniculata*, *T. Galeottiana*, and *T. heliocarpoides*) is of great interest in that though the three are definitely uncinate, they do not show any close affinity with any other species of the series. However, there is a very remarkable similarity between this complex and the *Calderoni* complex in Geniculatae. The two complexes have the same type of inflorescence, flowers of the same shape and structure, and fruits whose superficial resemblance is rather striking despite the fact that all species of the *Galeottiana* complex have essentially glabrous fruits. All species in the *Calderoni* complex have 2-merous ovaries, and *T. paniculata* bridges this difference in possessing a 4-loculate fruit. The affinity is further strengthened by the

tendency of *T. paniculata* to a tree habit, its numerous stamens, and its relatively large fruit. *T. Galeottiana* and *T. heliocarpoides* are not only closely related species but are also very closely allied with *T. paniculata*. Though the three are distinct, sometimes the delimitation of the species becomes very difficult especially when immature fruiting specimens are being considered. Both *T. Galeottiana* and *T. heliocarpoides* attain gynodioecism.

The *Bartramia* complex, consisting of four species, *T. sericata*, *T. brachistacantha*, *T. Bartramia*, and *T. Sampaioi*, is really problematic in its relationships. In the possession of cymes in dense nodose clusters the species resemble those of the *Galeottiana* complex, but, on the other hand, the oblongoid floral buds and pubescent fruits make them resemble the *semitriloba* complex. The picture is further complicated by the fact that *T. Bartramia* is a pantropic weed which is equally at home in both the eastern and western hemispheres. Though the complex does not attain gynodioecism, there is considerable reduction in the floral parts and in the size of the fruits, which are the smallest known for the American species. The fact that *T. Sampaioi* lacks an urceolus and has only five stamens places it in approximately the same degree of advancement and specialization as *T. Lappula*. *T. sericata* resembles *T. bogotensis* in having the same general type of flowers and indument, but has much smaller fruits with glabrous spines. *T. brachistacantha* has characters which are about intermediate between those of *T. sericata* and *T. Bartramia*. The relationships of the species of the *Bartramia* complex with those of the western hemisphere are not too apparent. Its affinity may be with either the *semitriloba* or *Galeottiana* complexes, or possibly with both.

From the above discussion of some of the salient characters and relationships of the species, it is quite obvious that no definition of the series could be given which would suit all the species. The characters are superposed in such a manner that hardly any two are correlated. I am unable to give any precise definition of the series as there are nearly as many exceptional forms as there are typical ones. Further, an attempt at classifying the genus based on characters derived from the size of the flowers, types of inflorescences or the nature of the stigmas (as suggested by Hochreutiner[31]) leads one into similar dilemmas.

Because of these apparent reticulate combinations of the characters, I am led to the conclusion with the original authors that the "series, though very useful for the purposes of a *clavis*, do not coincide with natural groups, but appear to represent three of the phylogenetic stages through which many species of section LAPPULA have passed, the stellate arrangement being the most primitive and the uncinate the most highly modified."[32] The three series are here maintained not only for the sake of convenience, but because they are the nearest approach to the real relationship of the species.

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[31] Ann. Conserv. Jard. Bot. Genève 18:92. 1914.
[32] Sprague & Hutch. Jour. Linn. Soc. Bot. 39:240. 1909.

Chromosome Counts

Chromosome counts were made for the following three species:

Triumfetta Bartramia	2n	32
Triumfetta Calderoni	2n	32
Triumfetta semitriloba	2n	32

The counts were made from root-tips of plants raised in a greenhouse at Missouri Botanical Garden. The seeds for *T. Calderoni* were collected by Dr. Edgar Anderson from Honduras, and those for *T. Bartramia* and *T. semitriloba* were sent to me by Dr. Brandao-Joly from São Paulo, Brazil. As none of the plants flowered meiotic counts could not be made.

Acknowledgments

I have been able to examine specimens, including many valuable types, from several major herbaria in Europe and North America and South America. The herbaria where specimens have been obtained for study, together with the symbols[33] employed in their citations are as follows:

BR Jardin Botanique de l'État Bruxelles.
C Universitetes Botaniske Museum, Copenhagen.
FM Chicago Natural History Museum, Chicago.
G Institut de Botanique Systematique de l'Université, Genève.
GH Gray Herbarium of Harvard University, Cambridge, Mass.
K Herbarium Royal Botanical Gardens, Kew.
MICH University of Michigan Herbarium, Ann Arbor.
Mo Herbarium Missouri Botanical Garden, St. Louis.
NY Herbarium New York Botanical Garden, New York.
P Muséum National d'Histoire Naturelle, Paris.
R Museu Nacional, Rio de Janeiro.
S Naturhistoriska Riksmuseet, Stockholm.
TRIN Herbarium Department of Agriculture, Port of Spain, Trinidad.
U Botanisch Museum en Herbarium, Utrecht.
UC University of California Herbarium, Berkeley.
US U. S. National Herbarium of Smithsonian Institution, Washington, D. C.

Dot maps have been prepared from most of the specimens from which the exact locality could be determined. In the Index to Exsiccatae all the numbered and most of the unnumbered collections have been cited.

I wish to acknowledge my indebtedness to the curators of the institutions mentioned above, and to the Director of Missouri Botanical Garden, where this study was made. For illustrations and aid in chromosome counts I am indebted to Marilyn Amy Gage. Particular thanks are due to Dr. R. E. Woodson, Jr., for his advice, guidance, and constructive criticism.

Taxonomy

Triumfetta L. Sp. Pl. ed. 1. 444. 1753; DC. Prod. 1:506. 1824; K. Schum. in Mart. Fl. Bras. 12^3:131. 1886, in Engl. & Prantl, Nat. Pflanzenfam. 3^6:28. 1895; Sprague & Hutch. in Jour. Linn. Soc. Bot. 39:231. 1909; Hochr. in Ann. Conserv. Jard. Bot. Genève 18:92. 1914.

Bartramia L. Sp. Pl. ed. 1. 389. 1753.

[33] The symbols used are as suggested by Lanjouw in Chron. Bot. 5:143. 1939.

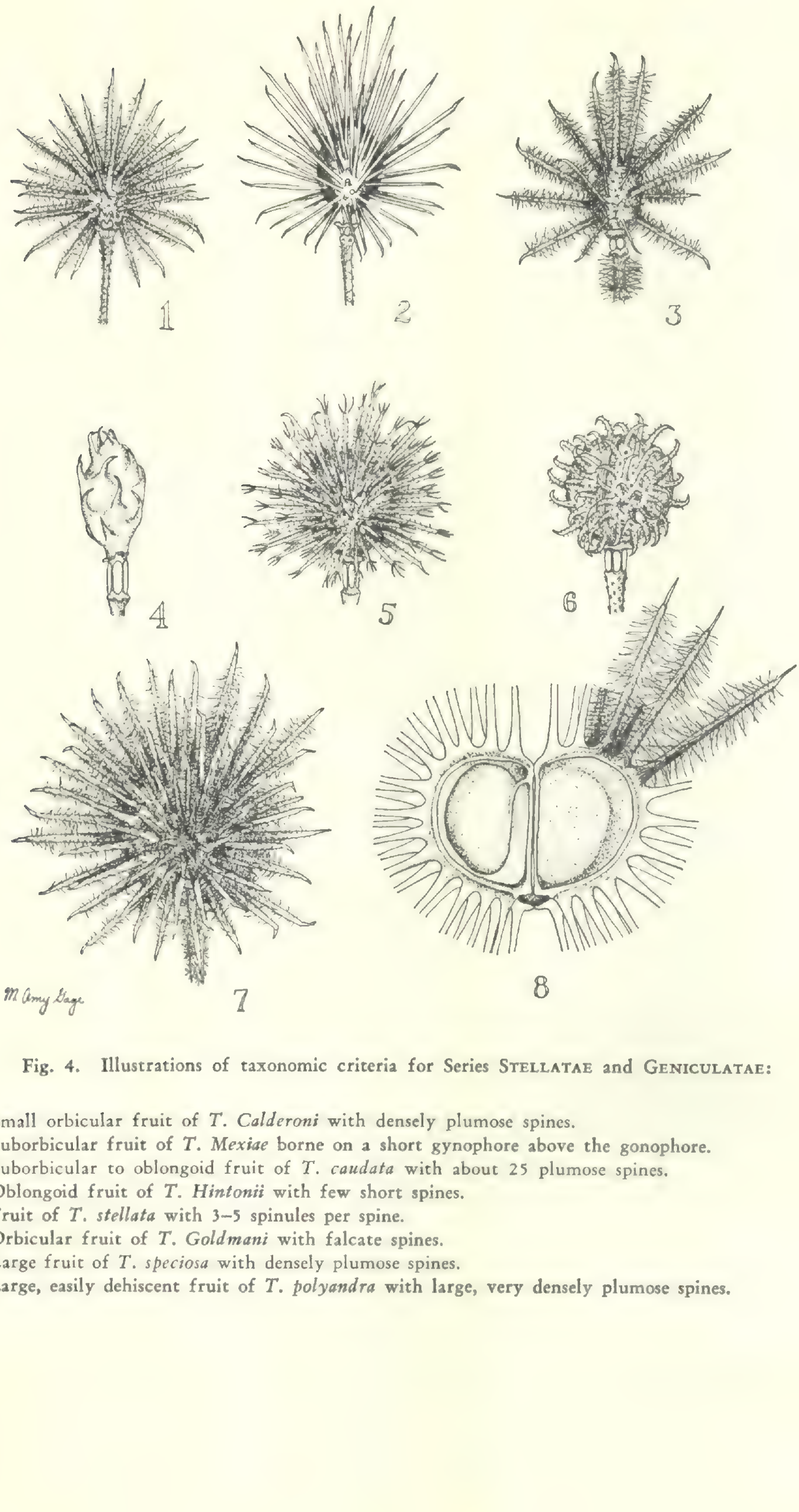

Fig. 4. Illustrations of taxonomic criteria for Series STELLATAE and GENICULATAE:

1. Small orbicular fruit of *T. Calderoni* with densely plumose spines.
2. Suborbicular fruit of *T. Mexiae* borne on a short gynophore above the gonophore.
3. Suborbicular to oblongoid fruit of *T. caudata* with about 25 plumose spines.
4. Oblongoid fruit of *T. Hintonii* with few short spines.
5. Fruit of *T. stellata* with 3–5 spinules per spine.
6. Orbicular fruit of *T. Goldmani* with falcate spines.
7. Large fruit of *T. speciosa* with densely plumose spines.
8. Large, easily dehiscent fruit of *T. polyandra* with large, very densely plumose spines.

Shrubs or trees. Leaves alternate, petiolate, stipulate, the stipules usually large, persistent, rarely fugacious, the blade 3- to 5-lobed or undivided, the venation palmate, 5- to 7-costate at the base. Inflorescences hermaphrodite or gynodioecious, usually axillary (terminal in few species), consisting of numerous aggregate dichasia. Flowers either hermaphrodite or pistillate, staminate ones not known, hypogynous, 5-merous; sepals 5, valvate, free, with apical appendages; petals 5, sometimes absent, free, imbricate, 3- to 5-nerved, shorter than the sepals, usually ciliate at the base (claw); gonophore bearing 5 spherical or elongate glands manifest, absent in some species, usually crowned by a ciliate, rather membranaceous ring (urceolus) surrounding the stamens; stamens 5–60 in hermaphrodite flowers, staminodial or absent in the pistillate, borne cyclically on the enlarged gonophore, with 2 thecous, 4-celled, introrse, longitudinally dehiscent anthers, the filaments free, usually glabrous, sometimes pubescent at the base, often with retrorse serrations; ovary wholly superior, sessile on the gonophore (except in *T. Mexiae*, with very short gynophore on the gonophore), ellipsoid to orbicular, covered with many short, either erect or recurved, hyaline spinules, 2- or 3-loculate, each with 2 anatropous collateral pendulous ovules, the style filiform, the stigma briefly 2- or 3-parted, sometimes capitate. Fruits dry, indehiscent or loculicidally dehiscent, 2- or 3-loculate, each cell 2-seeded, or falsely 6- to 9-loculate, or each cell 1-seeded, or 1-loculate with 1 seed due to abortion, usually sessile on the slightly accrescent gonophore, lappaceous, the spines elongating from the pericarp at the bases of the spinules; seeds compressed-ovoid or pyriform, with a more or less prominent funicular groove, the cotyledons folded, the endosperm oily.

Standard species: *Triumfetta Lappula* L.

KEY TO THE SERIES

A. Hyaline spinules of ovary straight, in fruit either straight or slightly deflexed, or consisting of 3–5 stellately arranged; ovaries 2-merous; stamens 20–60, most of the species with 40 or more; usually small trees 3–5 m. tall.
  B. Each spine with 3–5 stellately arranged spinules; mature floral buds pandurate ..... Stellatae (p. 334).
  BB. Each spine with 1 straight or slightly deflexed spinule; mature floral buds oblongoid or obovoid ..... Geniculatae (p. 336)
AA. Hyaline spinules of ovaries and fruits arcuately recurved; ovaries 3- or rarely 2-merous; stamens 5–40, most of the species with less than 30; usually shrubs 1–3 m. high ..... Uncinatae (p. 349)

Series Stellatae Sprague & Hutch. in Jour. Linn. Soc. Bot. 39:240. 1909.

1. Triumfetta **stellata** Ko Ko Lay, sp. nov.

Arbores parvae 3 m. altae. Ramuli graciles dense stellato-pubescentes. Folia anguste ovata interdum obscure 3-lobata 5–6 cm. longa 2–3 cm. lata ad basim subtruncata vel subcordata longe acmuinata subdupliciter serrata utrinque pilis sparsis stellatis; petiolis 1–3 cm. longis pilis fulvis stellatis pubescentibus. Inflorescentiae axillares, cymis cymulis 4–5, pedunculis plerumque 4–6 mm. longis, pedicellis 2–3 mm. longis. Flores hermaphroditi, alabastro maturo pandurato 8–9

Fig. 5. *Triumfetta stellata*

mm. longo; sepalis ellipticis circiter 10 mm. longis extra minute stellato-puberulentis, appendiculis circiter 0.25 mm. longis; petalis obovatis brevissimis 2–3 mm. longis, unguilo 1.0–1.5 mm. longo extra breviter villoso; gonophoro circiter 1.5 mm. longo, glandulis ellipticis circiter 1.0 mm. longis 0.5 mm. latis; urceolo 0.3 mm. alto 5-lobato breviter ciliato; staminibus 25–30, filamentis usque ad 5–7 mm. longis glabris; ovario breviter oblongo-ellipsoideo circiter 1 mm. longo, spinulis 35–40 erectis, stylo glabro 2–3 mm. longo, stigmate breviter 2-fido. Fructus globosi non dehiscentes, corpore ipso 3 mm. diametro 2-loculari, loculis 1-spermis cano-tomentosis, aculeis 2–3 mm. longis inaequilater breviter pubescentibus, spinulis 3–5 per aculeo; seminibus maturis haud visis.

MEXICO: MÉXICO: Temascaltépec, Las Mesas, alt. 2000 m., Oct. 25, 1933, *Hinton 4460* (HOLOTYPE in Herb. Kew.).

The affinities of this very distinct species are doubtful. It has a superficial resemblance to *T. Galeottiana*, but can be recognized easily in fruit by the 3 to 5 stellately arranged spinules on the spines, and in flower by its pandurate floral buds with very small obovate petals, which also have small foveae at about the tip of the claw.

Series Geniculatae Sprague & Hutch. in Jour. Linn. Soc. Bot. 39:240. 1909.

KEY TO THE SPECIES

A. Sepals at anthesis 2–4 cm. long; mature fruit body 4–10 mm. in diameter.
  B. Sepals at anthesis 3.5–4.0 cm. long, the apical appendages 1–3 mm. long; spines 4 mm. long or more, densely plumose.
    C. Leaves broadly elliptical to obovate, the petioles about 1 cm. long or less; petals broadly obovate, subequalling the sepals; fruit easily dehiscent, 1.2–3.0 cm. wide including the spines, the spines 0.6–1.0 cm. long; southern Mexico and Honduras ..... 2. *T. polyandra*
    CC. Leaves ovate to 3-lobed, the petioles 3–5 cm. long; petals elliptical, less than half the length of the sepals; fruit indehiscent, 1.0–1.5 cm. wide including the spines, the spines 3–5 mm. long; southern Mexico to Panama ..... 3. *T. speciosa*
  BB. Sepals at anthesis 2.0–2.5 cm. long, the apical appendages about 1 mm. long; spines 2–3 mm. long, lightly pubescent to glabrescent (not known in *T. cucullata*).
    C. Leaves 11–15 cm. long, the petioles with 2–4 prominent spherical glands at the basal sinus; petals broadly obovate, about 22 mm. long.
      D. Leaves elliptical, acute, the petioles about 1.5 cm. long; stamens 20; coastal west-central Mexico ..... 4. *T. cucullata*
      DD. Leaves broadly ovate to 3-lobed, acuminate, the petioles 4–6 cm. long; stamens 40; southwestern Mexico ..... 5. *T. coriacea*
    CC. Leaves 5–7 cm. long, the petioles without glands at the basal sinus; petals elliptical to narrowly obovate, 1.2–1.6 cm. long; western Mexico ..... 6. *T. Goldmani*
AA. Sepals at anthesis 0.4–1.6 cm. long; mature fruit body 2–3.5 mm. in diameter.
  B. Sepals at anthesis 1.0–1.6 cm. long; fruit body oblongoid, the spines 25 or fewer.
    C. Stem and petioles densely ferruginous-tomentose; leaves pubescent on both surfaces, densely so beneath; sepals densely tomentose without; mature fruit tomentose, 2-loculate, the spines 3–5 mm. long; Colombia ..... 7. *T. caudata*
    CC. Stem and petioles glabrescent; leaves essentially glabrous on both surfaces; sepals nearly glabrate without; mature fruit glabrate, 1-loculate, the spines 1–2 mm. long; central Mexico .... 8. *T. Hintonii*
  BB. Sepals at anthesis 0.4–1.0 cm. long; fruit body globose or subglobose, the spines 50 or more.
    C. Petals 1–2 mm. long; leaves densely tomentose; spines plumose, the fruit densely tomentose (not known in *T. ferruginea*).
      D. Apical appendages of the sepals nearly obsolete; leaves cuneate to rounded at the base, rarely subcordate; Honduras and El Salvador ..... 9. *T. Calderoni*
      DD. Apical appendages of the sepals manifest; leaves distinctly cordate.
        E. Inflorescences hermaphrodite; sepals 7–10 mm. long; style 4–6 mm. long.
          F. Flowering peduncles 2–4 mm. long; floral buds obovoid; stamens 40–60.
            G. Apical appendages of the sepals 2–3 mm. long, plumose; stamens about 60; stigma undivided; southern Mexico.. 10. *T. ferruginea*

GG. Apical appendages of the sepals about 1 mm. long, lightly pubescent; stamens 40–50; stigma 2-lobed; Costa Rica and Panama..... 11. *T. arborescens*

FF. Flowering peduncles about 1 mm. long; floral buds oblongoid; stamens about 20; Colombia..... 12. *T. persimilis*

EE. Inflorescences gynodioecious; pistillate sepals 4–5 mm. long; style about 2 mm. long; southern Mexico..... 13. *T. dioica*

CC. Petals 3–7 mm. long; leaves glabrescent; spines and fruits glabrate (not known in *T. attenuata*).

D. Leaves long-attenuate, the veins on lower surfaces glabrate; sepals essentially glabrous without, the apical appendages about 2 mm. long; stamens 60; style about 6 mm. long; southern Mexico..... 14. *T. attenuata*

DD. Leaves shortly acute to acuminate, the veins on the lower surfaces pubescent; sepals lightly stellate-pubescent without, the apical appendages less than 1 mm. long to nearly obsolete; stamens 40; style about 2 mm. long; southwestern Mexico.... 15. *T. Mexiae*

2. TRIUMFETTA POLYANDRA DC. Prod. 1:508. 1824. (T.: based on Sessé & Mociño's *tab. 117* in Herb. Genève).[34]

Triumfetta obovata Schlecht. et Cham. in Linnaea 5:288. 1830. (T.: *Schiede & Deppe s. n.*).

Triumfetta insignis S. Wats. in Proc. Am. Acad. 22:400. 1887. (T.: *E. Palmer 152*).

Small trees or large shrubs about 3–4 m. high; branches and inflorescence axes very densely tomentose with long ferruginous hairs. Leaves broadly elliptical to obovate, 13–15 cm. long and 10–12 cm. wide, the base rounded or subcordate, the tip abruptly acuminate, doubly and regularly serrate, both surfaces scabrous, rather densely tomentose with both simple and stellate hairs; petioles short, stout, about 1 cm. long, covered rather densely with long hairs. Inflorescences on axillary and terminal branches, the cymes of 2–3 cymules, the flowering peduncles 5–9 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, the buds oblongoid, 30–35 mm. long slightly before anthesis, the apical appendages 1–3 mm. long; sepals narrowly obovate, about 36 mm. long, covered rather densely with many long coarse hairs without; petals broadly obovate, showy, 2.7–3.2 cm. long and 5–6 mm. wide, the claw 5–6 mm. long, densely plumose; gonophore short and stout, about 0.75 mm. long and 2.0 mm. thick, the glands oblong, subequalling the gonophore; urceolus about 0.75 mm. high, many-lobed, lightly ciliate; stamens 40–50, the filaments glabrous; ovary spheroid, 3 mm. long, the style 25–28 mm. long, the stigma acute. Fruit spherical, easily dehiscent, the body 6–10 mm. in diameter, densely plumose, 4-loculate, each 2-seeded, the spines numerous, 6–10 mm. long, densely plumose with long hyaline or ferruginous hairs, the spinules erect; seeds ovoid, about 2 mm. long and wide.

Rather rare plants which grow in open forests, usually upon rocky mountain slopes at altitudes of 800–1500 m. in southern Mexico and northern Honduras; flowering from August to September, the fruit maturing from late October and persisting on the plant until early December.

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[34] Hochr. in Ann. Conserv. Jard. Bot. Genève 18:110. 1914.

Mexico: chiapas: Chacomuselo, alt. 800 m., *Matuda 4436* (Mo). jalisco: Río Blanco, *E. Palmer 152* (Mo, US), *252* (US); slopes of barranca near Guadalajara, *Pringle 4469* (BR, Mo); bluffs near Guadalajara, alt. 5000 ft., *Pringle 9694* (Mo, US); on the road between Colotlán and Bolaños, *Rose 2822* (NY). méxico: Temascaltépec, Luvianos, alt. 1300 m., *Hinton 5900* (US). nayarit: Tépic, between Pedro Paula and Acuponeta, *Rose 1927* (NY). vera cruz: Mirador and vicinity, *Liebmann 512, 521* (US), alt. 3500 ped., *Linden Suppl. 26* (BR), *47* (BR, G); Cordillera, Zacuapán, alt. 2000–3000 ped., *Galeotti 7062* (BR).

Honduras: yoro: Aguan River valley, vicinity of Coyoles, alt. 1000 ft., *Yuncker, Koepper & Wagner 8167* (Mo).

This species is very distinct and can be easily recognized by its large showy flowers, the largest known for the genus, and also by the extremely characteristic large, easily dehiscent fruits with many long very plumose spines. De Candolle based his description on the sketch of Sessé and Mociño. I have seen a photograph of the original sketch and have no difficulty in recognizing that *T. insignis* of S. Watson is conspecific with it. I have not seen the type of *T. obovata*, but my interpretation of that species is based on the original description, which was later amplified by Turczaninow on Linden's Supplementary Collection No. 47, which I have seen.

3. Triumfetta speciosa Seem. Bot. Voy. Herald, 86. 1853. (T.: *Seemann 1240*).

Triumfetta macrocalyx Turcz. in Bull. Soc. Nat. Moscou 31[1]:230. 1858. (T.: *Linden Suppl. 25*).

Triumfetta micropetala Hochr. in Ann. Conserv. Jard. Bot. Genève 18:98. 1914. (T.: *Linden Suppl. 25*).

Small trees or large shrubs 3–4 m. high; branches and inflorescence axes scurfy, densely covered with ferruginous tomentum. Leaves broadly ovate, generally 3-lobed, 6–9 cm. long and 5–7 cm. wide, the base rounded or subcordate, the middle lobe long-attenuate, the laterals short and blunt, the serrations very irregular, usually blunt and often glandular, the upper surface dark green, coarse with many short stellate hairs, the lower pallid, densely tomentose; petioles 3–5 cm. long, lightly pubescent. Inflorescences axillary, the cymes of 1–2 cymules, usually opposite the bracts, the flowering peduncles 4–5 mm. long, the pedicels 6–8 mm. long. Flowers hermaphrodite, large, the buds oblongoid, 30–35 mm. long slightly before anthesis, the apical appendages about 2 mm. long; sepals narrowly elliptical, about 35 mm. long with many separate tufts of long stellate hairs without; petals ovate, short, about 6 mm. long, the claw about 3–4 mm. long, very densely plumose; gonophore about 1 mm. long and 2 mm. wide, the glands spherical, subequalling the gonophore; urceolus short, about 0.5 mm. high, many-lobed, lightly ciliate; stamens 20, the filaments glabrous; ovary ovoid, about 1.5 mm. long, the style 30–34 mm. long, with many short separate tufts of stellate hairs, the stigma acute. Fruit orbicular, the body 6–8 mm. in diameter, rather densely pubescent, 4-loculate, each cell 2-seeded, on maturity with 8 distinct 1-seeded locules, the spines numerous, 100 or more, each 3–4 mm. long, densely plumose with short hairs, the spinules erect; seeds ovoid, about 2.0 mm. long and wide.

A species of relatively scattered distribution, which extends from southern Mexico to Panama; usually growing in open areas on slopes of mountains, or along the rocky banks of streams at altitudes of 1300–1700 m.; flowering from late July to September, the fruit persisting on the plants until late February or March.

MEXICO: CHIAPAS: Siltepec, *Matuda 1581* (Mo). JALISCO: San Sebastián, trail to El Ranchito, alt. 1500 m., *Mexia 1444* (Mo, US). VERA CRUZ: Mirador, *Linden Suppl. 25* (BR, FM photo); Zacuapán and vicinity, *Purpus 1918* (Mo, NY, US), *3749* (Mo, UC); Cordillera, locality not mentioned, *Galeotti 1973* (BR), *4162* (BR).

BRITISH HONDURAS: Vaca Falls District, *Record s. n.* (US).

GUATEMALA: ALTA VERAPAZ: Patal, alt. 1600 m., *Tuerckheim II 1546* (Mo); San Cristóbal, *Tejada 265* (US).

HONDURAS: MORAZAN: La Montañita, alt. 1400 m., *Williams & Molina R. 10636* (Mo); Mt. Uyuca, alt. 1600 m., *Williams & Molina R. 10252* (Mo).

PANAMA: CHIRIQUÍ: Boquete, *Seemann 1240* (K); Volcán de Chiriquí, Boquete Distr., alt. 7000 ft., *Davidson 515, 895* (Mo); Finca Lérida to Boquete, alt. 1300–1700 m., *Woodson, Allen & Seibert 1115* (Mo).

This species is characterized by its very large flowers and disproportionally short petals, and also by its large fruits with briefly plumose spines. It is rather interesting to note that both the species of Turczaninow and Hochreutiner are primarily based on *Linden Suppl. 25*, a sheet which was apparently examined also by Seemann, as he cites a Linden collection from Vera Cruz, Mexico.

4. TRIUMFETTA CUCULLATA Fernald, in Bot. Gaz. 20:532. 1895. (T.: *Lamb 579*).

Shrubs about 2–3 m. high; lower branches sparingly pubescent, the upper and the inflorescence axes densely cinereous-tomentose. Leaves elliptical, about 13–15 cm. long and 4–5 cm. wide, the base obtuse, with 4 spherical glands at the basal sinus, the serrations generally glandular, the upper surface lightly stellate-pubescent, the lower more densely so; petioles 1.0–1.5 cm. long, densely tomentose. Inflorescences axillary, the cymes of 3 cymules, generally condensed, the flowering peduncles about 3 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 22–24 mm. long slightly before anthesis, constricted slightly above the base, the apical appendages slender, 0.5–1.0 mm. long, very lightly pubescent; sepals oblong, 22–25 mm. long including the apical appendages, stellate-tomentose without, glabrescent within; petals broadly obovate, about 23 mm. long and 6–7 mm. wide, the claw about 4–5 mm. long, densely plumose; gonophore short and stout, about 1.5 mm. long and 2–3 mm. wide, the glands quadrangular, broad, about 1.0 mm. long and 1.5 mm. wide; urceolus short, about 0.5 mm. high, distinctly many-lobed, briefly ciliate; stamens 20, the filaments smooth, densely pubescent at the base; ovary orbicular, about 1.5 mm. long, the spinules about 50, erect, the style about 22 mm. long, the stigma acute. Fruit not seen.

Known only from the type. Flowers in February.

MEXICO: NAYARIT: Tépic, Zopelote, alt. 2000–3000 ft., *Lamb 579* (Mo, US).

Though very imperfectly known, this species may be easily identified by its short-petiolate elliptic leaves, by its large showy flowers, and also by its possession of only 20 stamens with the filaments densely pubescent at the base.

5. Triumfetta coriacea Hochr. in Ann. Conserv. Jard. Bot. Genève 18:108. 1914. (T.: *Langlassé 815*).

Small trees or large shrubs 3–4 m. high; branches and inflorescence axes glabrescent, brownish. Leaves broadly ovate to 3-lobed, 11–14 cm. long and 8–12 cm. wide, the base cuneate to rounded, the tip long-acuminate; the serrations regular and usually double, the upper surface glabrate, the lower very lightly pubescent to glabrescent; petioles stout, 4–6 cm. long, with 2 or 4 prominent glands at the basal sinus. Inflorescences axillary, rarely terminal, the cymes of 2–3 cymules, borne very loosely in nodose clusters, the flowering peduncles 6–8 mm. long, the pedicels 2–4 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, about 22 mm. long slightly before anthesis, constricted in the middle, the apical appendages very short, about 0.5 mm. long; sepals elliptical, 22–24 mm. long, rather lightly stellate-pubescent without; petals broadly obovate, 20–22 mm. long and 6–8 mm. wide, the claw about 3 mm. long, densely plumose; gonophore slender, 1–2 mm. long, the glands elliptical, subequalling the gonophore; urceolus about 0.5 mm. high, many-lobed, lightly ciliate; stamens about 40, the filaments glabrous; ovary ovoid, about 1.5 mm. long, the spinules numerous, erect, the style about 22 mm. long, the stigma acute. Immature fruit orbicular, the body essentially glabrous, 2-loculate, each cell 1-seeded, the spines numerous, rather short; mature fruit not seen.

Southwestern Mexico, usually growing on hillsides in pine and oak forests at altitudes of 800–1000 m.; flowering from middle of December to late January.

Mexico: guerrero: San Vincente de San Juan, alt. 920 m., *Hinton 11193* (GH); Plan de Carrizo, Galeana, alt. 850 m., *Hinton 11056* (GH); Sierra Madre, alt. 800 m., *Langlassé 815* (G, GH, US).

This species can be recognized by its glabrescent, broadly ovate to 3-lobed leaves with 2–4 spherical glands on the petioles at the basal sinus; and also by its large, showy flowers with deep yellow broadly obovate petals. It is unfortunate that mature fruiting specimens are unavailable.

6. Triumfetta Goldmani Rose, in Contr. U. S. Nat. Herb. 12:285. 1909. (T.: *Goldman 264*).

Triumfetta sanctae-luciae Sprague, in Kew Bull. 114. 1923. (T.: *Seemann 2147*).
Triumfetta quercetorum Bullock, loc. cit. 295. 1937. (T.: *Hinton 6746*).

Small trees or large shrubs 3.0–3.5 m. high; branches and inflorescence axes with many short stellate hairs, later becoming glabrate. Leaves elliptical to narrowly ovate, 5–7 cm. long and 2–3 cm. wide, the base cuneate or rounded, the tip narrowly and gradually long-attenuate, the serrations rather regular, both surfaces scabrous with many short stellate and simple hairs; petioles slender, 1.0–1.5 cm. long, rather lightly but coarsely pubescent; bracts of the same general shape as the vegetative leaves. Inflorescences axillary, rarely terminal, the cymes of 1–2 cymules, always in the axils of the bracts, the flowering peduncles 4–6 mm. long, the pedicels about 4 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, 18–20 mm. long and 2–3 mm. wide slightly before anthesis, the apical

appendages slender, 1–2 mm. long; sepals narrowly ovate, about 20 mm. long, with few separate tufts of short stellate hairs without; petals elliptical to narrowly obovate, 12–16 mm. long and about 3 mm. wide, the claw 4–5 mm. long, densely plumose; gonophore large, about 2.5 mm. long and 1.5 mm. wide, the glands elliptical, subequalling the gonophore; urceolus short, about 0.25 mm. high, many-lobed, lightly ciliate; stamens 20, the filaments glabrous, ovary orbicular, about 1.5 mm. long, the spinules about 75, erect, the style about 16 mm. long, the stigma either acute or briefly bifid. Fruit spheroid, the body 4–5 mm. in diameter at maturity, lightly pubescent, 4-loculate, each cell 1-seeded, the spines falcate, about 75, 2–3 mm. long, lightly pubescent with few short hairs; seeds pyriform, about 1.5 mm. long and wide.

Rather common plant of western and central Mexico, usually growing in oak and pine forests in shady slopes under trees in moist places or on edges of meadows along streams at altitudes of 600 to 2000 m.; flowering in September and October, the fruit persisting until late January.

MEXICO: CHIHUAHUA: Arroyo Hondo, Sierra Charuco, *Gentry 1768* (Mo, US); San José de Pinál, Río Mayo, *Gentry 2841* (Mo); Guicorichi, Río Mayo, alt. 5000 ft., *Gentry 1967* (Mo); El Carrizo, alt. 800 m., *Ortega 6011* (US); Balboa, *Ortega 5043* (US). DURANGO: Sierra Tres Picos, alt. 3500 ft., *Gentry 5296* (Mo); La Bajada, Tamazula, alt. 300 m., *Ortega 4252* (US). GUERRERO: Mina, Zihuagio-Ojo de Agua, alt. 1640 m., *Hinton 9710* (US); Mina, Chiriagua, alt. 1600 m., *Hinton 9847* (GH), *10663* (GH, Mo, US); Pilas Filo Mayor, alt. 1800 m., *Hinton 10750* (GH, US); Chilacayote-Espadinas, alt. 1500 m., *Hinton 14927* (GH, US). MÉXICO: Temascaltepec: Rincón del Carmen, alt. 1340 m., *Hinton 1953* (Mo); Nanchititla, *Hinton 3082* (GH, K), *4962* (K); Pungarancho, alt. 950 m., *Hinton 5253* (Mo, US), *6746* (GH, K, Mo, US); Ypericones, *Hinton 6996* (Mo, US). MICHOACAN: Coalcomán: Salitre-mesa, alt. 1780 m., *Hinton 12492* (GH, US); Pto. Zarzamora, alt. 1660 m., *Hinton 12262* (GH, US). SINALOA: Santa Lucia, alt. 1200 m., *Seemann 2147* (GH, K); Sierra de Choix, 50 miles n. e. of Choix, *Goldman 264* (US); Cerro de la Sandia, northeast of Panuco, alt. 1800–2000 m., *Pennell 20121* (US); Quebrada de Mansana, Sierra Suratato, alt. 4000–4500 ft., *Gentry 6582* (Mo); Sierra Madre Mts., "El Batél", alt. 4000 ft., *Mexia 431* (Mo); Quebrada Chica, San Ignacio, alt. 1380 m., *Narvaez & Salazar 100* (US). SONORA: Arroyo del Agua Blanco, Dist. Álamos, *Gentry 506M* (US).

The fruits of this species are very characteristic, being spheroid with about 75 falcate, lightly pubescent spines. Though the spines are slightly recurved the spinules are erect. The small elliptical to narrowly ovate leaves and the relatively large flowers with yellow, narrowly obovate petals make this species convenient to identify. The leaves of the type of *T. quercetorum* are very slightly more pubescent than those of *T. Goldmani,* but in both they are nearly glabrate and the variation is only slight.

7. TRIUMFETTA CAUDATA Tr. & Planch. in Ann. Sci. Nat. Bot. IV, 17:353. 1862. (T.: "Río Hacha", *Purdie s. n.* in Herb. Kew.).

Small trees or shrubs 2–3 m. high; branches and inflorescence axes covered very densely with rich orange-brown simple and stellate hairs. Leaves broadly ovate, 11–15 cm. long and 8–10 cm. wide, the base rounded to subcordate, the tip gradually and narrowly long-attenuate, the serrations blunt, small, usually double and regular, the upper surface scabrous, lightly pubescent, the veins more

densely so, the lower rather densely tomentose with both stellate and simple hairs; petioles 3–5 cm. long, densely covered with orange-brown hairs. Inflorescences axillary, the cymes of 2–3 cymules, usually in the axils of the bracts, the flowering peduncles 4–5 mm. long, the pedicels 3–4 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, 10–15 mm. long slightly before anthesis, the apical appendages 1–2 mm. long, densely pubescent; sepals oblong, 12–16 mm. long with dense orange-brown pubescence without; petals narrowly obovate, subequalling the sepals, the claw 2–3 mm. long, rather densely plumose; gonophore short, about 0.5 mm. long, the glands small, spherical; urceolus about 0.5 mm. high, many-lobed, densely ciliate; stamens 20–25, the filaments glabrous; ovary ovoid, about 0.75 mm. high, the spines 40–50, erect, the style 7–8 mm. long, the stigma acute. Fruits oblongoid, the body 2–3 mm. in diameter and 3–5 mm. long at maturity, densely pubescent with many short stellate and simple hairs, 2-loculate, each cell 1-seeded, the spines 20–25, each 3–5 mm. long, densely plumose with short grayish hairs; seeds ovoid, about 1.5 mm. long and wide.

Apparently rare plants known only from Colombia, where they grow on the borders of forests and open grasslands at altitudes of about 750 m.; flowering from October to December, and the fruits maturing in January and February.

Colombia: magdalena: près de Molina, Río Hacha, *Purdie s. n.* (K); Minca, *Apolinar 627* (US). santa marta: Onaca, alt. 2500 ft., *H. H. Smith 1688* (G, Mo, NY, UC, US), *1907* (Mo, NY).

This is an extremely distinct species, and is characterized by its branches and petioles being densely covered with lustrous ferruginous tomentum, by the leaves which are profoundly cordate with long attenuate tips, by the large and spreading inflorescences, and also by its small ellipsoid fruits with about 25, rather densely tomentose spines.

8. Triumfetta Hintonii Sprague, in Kew Bull. 294. 1937. (T.: *Hinton 7018*).

Small trees 2.5–6.0 m. high; branches and inflorescence axes very lightly pubescent, glabrescent. Leaves broadly ovate to elliptical, 8–11 cm. long and 3–5 cm. wide, the base cuneate to rounded on younger ones, subcordate on more mature ones, the tip gradually and narrowly acuminate, the serrations small, blunt, usually double and regular, the upper surface dark green, very lightly pubescent to nearly glabrate, the lower pallid, slightly more pubescent than the upper; petioles 2–3 cm. long, lightly pubescent. Inflorescences axillary, the cymes of 2 cymules, usually opposite the bracts, the flowering peduncles 3–5 mm. long, the pedicels 2–3 mm. long. Flowers hermaphrodite, the buds oblongoid, 9–11 mm. long at anthesis, the apical appendages very small, nearly obsolete; sepals oblong, 10–12 mm. long, lightly stellate-pubescent without; petals narrowly obovate, 6–7 mm. long, the claw very distinct with a constriction at the tip, about 3 mm. long, densely plumose; gonophore slender, about 2 mm. long, the glands oblong, about half the length of the gonophore; urceolus short, about 0.5 mm. high, 5-lobed, lightly ciliate; stamens 15–20, the filaments smooth, glabrous; ovary ellipsoid, about 1.5 mm. long, the spinules 40–50, erect, the style about 6 mm. long, the

stigma acute, sometimes briefly 2-lobed. Fruit ellipsoid, the body about 6 mm. long and 3.0–3.5 mm. wide at maturity, glabrous, 2-loculate, each cell 1-seeded, but only one maturing, the other aborting completely, the spines slightly falcate, short, 1–2 mm. long, only 10–16 remaining at maturity; seeds pyriform, about 2.5 mm. long and 1.5 mm. wide.

Known only from central Mexico, growing in pine and oak forests, along streams at altitudes of 2000–2400 m.; flowering from June to September, the fruit maturing from October to November.

MEXICO: MÉXICO: Temascaltépec: La Labór, alt. 2000 m., *Hinton 3837* (K, US); Cajones, alt. 2480 m., *Hinton 4224* (K); Nanchititla, *Hinton 5324* (K, US); La Labór, *Hinton 6594* (GH, Mo, US); Cumbre de Tejupilco, *Hinton 7018* (K, Mo, US); Pantoja, *Hinton 7027* (Mo, US). MICHOACAN: Coalcomán, Sierra Torricillas, alt. 2140 m., *Hinton 12343* (GH).

This species has very characteristic fruits. The flower is quite normal for the genus, bearing a 2-loculate ovary with 40–50 straight-pointed spinules. After fertilization, most of the spines fail to develop at the bases of the spinules; thus the mature fruit body becomes rugose in places where the spines have not elongated sufficiently; furthermore, one of the locules aborts completely, and only one 1-seeded locule matures. In their oblongoid fruits and also in their marked tendency towards having a smaller number of spines on the fruit than of spinules on the ovaries, *T. Hintonii* and *T. caudata* are closely related.

9. TRIUMFETTA CALDERONI Standl. in Jour. Wash. Acad. 14:98. 1924. (T.: *Calderón 78*).

Small trees or large shrubs 6–8 m. high; branches and inflorescence axes covered densely with both fine stellate and long spreading coarse stiff hairs. Leaves broadly ovate to obscurely 3-lobed, 10–15 cm. long and 7–11 cm. wide, the base rounded or subcordate, the tip gradually and narrowly long-acuminate, the serrations coarse and irregular, blunt and usually glandular, the upper surface dark green, lightly but coarsely pubescent with many short suppressed stellate hairs, the lower pallid, densely pubescent with long spreading stellate and simple hairs; petioles 5–7 cm. long, densely pubescent; bracts elliptical. Inflorescences terminal, large and spreading, with many small, caducous bracts, the cymes of 4–6 cymules, rather lax in flower though generally crowded in fruit, the flowering peduncles about 3–4 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, the buds broadly obovoid, constricted towards the base, about 5 mm. long at anthesis, the apical appendages very small to nearly obsolete; sepals elliptical, 5–7 mm. long, whitish and densely tomentose without, yellow-brown and glabrescent within; petals obovate, small, about 2 mm. long, the claw very short, lightly plumose; gonophore short and stout, about 0.5 mm. long and 1.5 mm. wide, the glands very small, spherical; urceolus about 0.25 mm. high, many-lobed, lightly ciliate; stamens 40, the filaments glabrous; ovary ovoid, about 1 mm. long, the spinules about 50, erect, the style 2–3 mm. long, the stigma acute. Fruit spheroid, the body 2–3 mm. in diameter at maturity, rather densely tomentose, 2-loculate, each cell 1-

seeded, the spines about 50, 4–5 mm. long, densely plumose with relatively long stiff white hairs; seeds pyriform, about 1.0 mm. long and wide.

Common weedy plant of Honduras and El Salvador, chiefly found in dry rocky thickets at altitudes of 450–1000 m.; flowering in October, the fruit maturing in late December to January.

Honduras: cholutecа: San Marcos, alt. 1000 m., pine forest area, *Williams & Molina R. 10923* (Mo). el paraíso: 8 kms. west of Ojo de Agua, *Williams & Molina R. 10676* (Mo). morazán: San Antonio, road near Zamorano, *Williams & Molina R. 11160* (Mo).

El Salvador: san josé: *Calderón 1929* (GH, US). san salvadór: vic. Tonacatepeque, *Standley 19475* (GH, US); vicinity of San Salvadór, alt. 650–850 m., *Standley 22782* (GH, US); San Salvadór, *Calderôn 78* (GH, US), *354* (US), *1257* (GH, Mo, US). data incomplete: *Choussy 55* (US).

This species can be recognized in fruit by its long slender, rather densely plumose spines, and in flower by the absence of apical appendages on the sepals, and also by the short petals.

10. Triumfetta **ferruginea** Ko Ko Lay, sp. nov.

Ramuli graciles dense pubescentes pilis ferrugineis et stellatis et simpilicibus. Folia late ovata interdum 3-lobata 6–7 cm. longa 5–7 cm. lata base profunde cordata apice longe acuminata supra pilis sparsis stellatis, infra dense canescentia vel ferrugineo-tomentosa; petiolis 3–4 cm. longis dense ferrugineo-tomentosis. Inflorescentiae terminales, cymis circiter 6 cymulis in axillis bractearum dense confertis, bracteis ellipticis vel lanceolatis, pedunculis plerumque 3 mm. longis, pedicellis 1–2 mm. longis. Flores hermaphroditi, alabastro maturo obovoideo 6–7 mm. longo; sepalis ellipticis 7–9 mm. longis extra breviter denseque stellato-pubescentibus, appendiculis circiter 2 mm. longis dense plumosis; petalis obovatis brevissimis 1.5–2.0 mm. longis, unguilo circiter 0.5 mm. longo extra dense plumosa; gonophoro circiter 0.5 mm. longo 1.5 mm. lato, glandulis quadrangularibus circiter 1.0 mm. longis; urceolo 0.5 mm. alto multilobato breviter ciliato; staminibus 60, filamentis usque 3–4 mm. longis glabris; ovario ovoideo circiter 1 mm. longo, spinulis 30–40 erectis, stylo glabro circiter 4 mm. longo, stigmate acuto. Fructus maturi desunt.

Mexico: chiapas: Las Pilas, June 2, 1904, *Goldman 1050* (holotype in U. S. Nat. Herb.).

Related to *T. arborescens* from which it may be easily distinguished by its more numerous stamens and much longer apical appendages of the sepals. I have not seen any fruiting specimen of this species.

11. Triumfetta arborescens (Seem.) Sprague, in Kew Bull. 351. 1923.

Heliocarpus arborescens Seem. Bot. Voy. Herald, 86. 1853. (T.: "Panama," *Seemann s. n.* in Herb. Kew.).

Small trees 5–6 m. high; branches and inflorescence axes scurfy, densely tomentose with short ferruginous stellate hairs. Leaves broadly ovate, usually 3-lobed, 10–13 cm. long and 7–10 cm. wide, the base cordate, the middle lobe long-

Fig. 6. *Triumfetta ferruginea*

attenuate, the laterals acute, the serrations very irregular, the basal ones glandular, the upper surface scabrous, covered lightly with many short stellate hairs, the lower densely tomentose with both simple and stellate hairs, becoming less so at maturity; petioles slender, 6–9 cm. long, densely ferruginous-tomentose. Inflorescences terminal, the cymes of 3–5 cymules, condensed in nodose clusters, the flowering peduncles 2–4 mm. long, the pedicels about 2 mm. long. Flowers hermaphrodite, the buds obovoid, 6–7 mm. long slightly before anthesis, constricted towards the base, the apical appendages about 1 mm. long; sepals broadly

elliptical, 7–10 mm. long, pallid and densely tomentose without, yellow-brown and glabrescent within; petals obovate, short, about 2–3 mm. long, the claw very short, briefly plumose; gonophore slender, about 0.75 mm. long, the glands elliptical, subequalling the gonophore; urceolus about 0.5 mm. high, indistinctly lobed, briefly ciliate; stamens about 50, the filaments smooth, glabrous; ovary ovoid, about 0.75 mm. long, the spinules about 75, erect, the style about 5 mm. long, the stigma very briefly 2-fid. Fruit suborbicular, the body 2–3 mm. in diameter and 3–4 mm. long at maturity, cinereous-pubescent, 2-loculate, each cell 1-seeded, the spines about 75, 3–4 mm. long, reddish-brown, shortly plumose; seeds pyriform, about 0.75 mm. long and wide.

Costa Rica: guanacaste: vicinity of Tilarán, alt. 500–650 m., *Standley & Valerio 45709* (US).

Panama: coclé: between Paso del Arado and Olá, in savannahs and thickets, alt. 20–280 m., *Pittier 5017* (US). data incomplete: *Seemann 96* (GH), *s. n.* (K); *Cowell 239* (NY).

Rather rare small trees of Costa Rica and Panama; flowering in December and the fruit maturing in January and February.

12. Triumfetta **persimilis** Ko Ko Lay, sp. nov.

Frutex circiter 1 m. altus. Ramuli graciles dense pubescentes, pilis ferrugineis et stellatis et simplicibus. Folia late ovata vel 3-lobata 10–14 cm. longa 8–10 cm. lata base profunde cordata apice longe acuminata margine irregulariter serrata interdum glandulosa supra pilis sparse stellatis scabratis, infra dense canescenti-tomentosa; petiolis 3–4 cm. longis dense tomentosis. Inflorescentiae terminales, cymis 3–4 cymulis, bracteis ovatis vel obscure 3-lobatis, pedunculis circiter 1 mm. longis, pedicellis 6–8 mm. longis. Flores hermaphroditi, alabastro maturo oblongoideo 6–8 mm. longo; sepalis ellipticis 7–9 mm. longis extra longe et dense stellato-tomentosis, appendiculis circiter 2 mm. longis dense plumosis; petalis ellipticis, 6–7 mm. longis, unguilo 0.5–1.0 mm. longo extra breviter plumoso; gonophoro circiter 0.25 mm. longo, glandulis quadrangularibus; urceolo 0.25 mm. alto, 5-lobato breviter ciliato; staminibus 20, filamentis usque ad 5–6 mm. longis glabris; ovario ovoideo circiter 1.5 mm. longo, spinulis 70–80 erectis, stylo glabro 3–4 mm. longo, stigmate breviter 2-fido. Fructus globosus non dehiscens, corpore ipso 2–3 mm. diametro, dense canescenti-tomentosus 2-locularis, loculis 2-spermis, aculeis circiter 75, 3–4 mm. longis dense plumosis; seminibus ovoideo-acutis, circiter 1.5 mm. longis et latis.

Colombia: santander: en terrenos secos y arenosos a orillas del Río Chicamocha, en pescadero, alt. 500 m., Dec. 1948, *Araque & Barkley 18S.286* (holotype in Herb. Mo. Bot. Gard., isotype in U. S. Nat. Herb.).

In flower this species has a superficial resemblance to *T. caudata,* but its fruits are much more strikingly similar to those of *T. Calderoni.* It may be easily recognized by its densely tomentose leaves, small oblongoid floral-bud with only 20 stamens, and by its spheroid fruit with many densely plumose spines.

13. TRIUMFETTA DIOICA T. S. Brandg. in Univ. Calif. Publ. Bot. 10:412. 1924. (T.: *Purpus 9256*).

Small trees about 3 m. high; branches and inflorescence axes covered densely with many long grayish-brown hairs. Leaves broadly ovate to obscurely 3-lobed, 8–11 cm. long and 5–7 cm. wide, the base deeply cordate, the tip gradually and narrowly long-acuminate, the serrations very irregular, usually blunt, the basal ones glandular, the upper surface dark green, scabrous with many long appressed simple and stellate hairs; petioles 4–6 cm. long, slender, densely clothed with long spreading hairs. Inflorescences gynodioecious, the pistillate terminal, the cymes of 4–6 cymules in dense nodose clusters, the flowering peduncles and pedicels about 2 mm. long. Hermaphrodite flower not seen, the pistillate small, the floral bud 3–4 mm. long slightly before anthesis, the apical appendages short, 1 mm. long or less; sepals narrowly elliptical, 4–5 mm. long, pallid and densely tomentose without, yellow-brown and glabrescent within; petals elliptical to narrowly obovate, small, about 1.5 mm. long, the claw nearly obsolete; gonophore short, about 0.5 mm. long, the glands oblong, subequalling the gonophore; urceolus about 0.5 mm. high, many-lobed, briefly ciliate; ovary ovoid, about 1.5 mm. long, the spinules about 50, erect, the style about 2 mm. long, the stigma briefly 2-fid. Fruit spheroid, covered with about 50 slender, densely plumose spines; mature fruit not seen.

Known only from Chiapas, Mexico. Flowers in September.

MEXICO: CHIAPAS: Hacienda Monserrate, *Purpus 9256* (Mo, UC, US); Buena Vista, *Purpus 9285* (UC).

It is unfortunate that this species is so imperfectly known. Due to the lack of mature fruits and hermaphrodite flowers its proper position is rather obscure. It is apparently related to *T. Calderoni* in the possession of small flowers and spheroid fruits with numerous plumose spines.

14. TRIUMFETTA **attenuata** Ko Ko Lay, sp. nov.

Ramuli glabri irregulariter punctati lenticellis multis parvis tecti. Folia late ovata 10–14 cm. longa 6–9 cm. lata base subtruncata vel rotundata apice longe attenuata subdupliciter serrata utrinque glabrata; petiolis gracilibus 6–9 cm. longis glabris. Inflorescentiae terminales, cymis 4–5 cymulis, pedunculis 5–7 mm. longis, pedicellis 4–5 mm. longis. Flores hermaphroditi, alabastro maturo obovato 6–7 mm. longo; sepalis ellipticis vel anguste obovatis 7–9 mm. longis extra glabrescentibus, appendiculis circiter 2 mm. longis glabris; petalis obovatis 6–7 mm. longis, unguilo circiter 1.5 mm. longo dense plumoso; gonophoro circiter 0.75 mm. longo 1.5 mm. lato, glandulis ellipticis 0.5–0.75 mm. longis; urceolo 0.5 mm. alto 5-lobato breviter ciliato; staminibus 60, filamentis usque ad 5–7 mm. longis glabris, spinulis circiter 75 erectis, stylo glabro circiter 6 mm. longo, stigmate acuto. Fructus maturi desunt.

MEXICO: CHIAPAS: Escuintla, Dec. 1936, *Matuda 0488* (holotype in Herb. Mo. Bot. Gard.; isotypes in Herb. Univ. Michigan, and U. S. Nat. Herb.).

This species is most closely related to *T. Mexiae,* from which it may be distinguished easily by its glabrate leaves and floral buds, the much longer apical appendages of the sepals, and its style which is about 6 mm. long with the stigma exserted above the stamens. It is unfortunate that no fruiting material of this species is available.

15. Triumfetta **Mexiae** C. V. Morton & Ko Ko Lay, sp. nov.

Arbores parvae 5–6 m. altae. Ramuli inferne glabrati apicem versus tomentosi pilis multis brevibus stellatis. Folia late ovata 8–11 cm. longa 6–9 cm. lata base cuneata vel rotundata apice longe acuminata subdupliciter serrata utrinque pilis sparsis stellatis mox glabrescentia, nervis subtus pallidioribus pilis brevibus stellatis; petiolis 3–5 cm. longis sparse stellato-pubescentibus. Inflorescentiae terminales, cymis cymulis 4–5, pedunculis 2–3 mm. longis, pedicellis 3–4 mm. longis. Flores hermaphroditi, alabastro maturo obovoideo 5–6 mm. longo; sepalis anguste obovatis 5–8 mm. longis extra breviter stellato-pubescentibus; petalis ellipticis vel anguste obovatis 4–6 mm. longis, unguilo circiter 2 mm. longo dense plumoso; gonophoro circiter 0.75 mm. longo 1.0 mm. lato, glandulis ellipticis circiter 0.75 mm. longis; urceolo 0.25 mm. alto multilobato breviter ciliato; staminibus 40, filamentis usque ad 3–4 mm. longis glabris; ovario ovoideo circiter 1.5 mm. longo, stigmate breviter 2-fido. Fructus globosi non dehiscentes, gynophoro brevi supra gonophorum, corpore ipso 3–4 mm. diametro glabro 2-loculari, loculis 2-spermis, aculeis 75–100 gracilibus glabris; seminibus ovoideo-acutis circiter 2 mm. longis et latis.

A rather common species of southwestern Mexico, growing at altitudes of 1000 to 1200 m.; flowering in September and early October, the fruits maturing from late October to November.

Mexico: guerrero: Sierra Madre del Sur, north of Río Balsas, Distr. Adama, Temisco, barranca below Ore Mill, alt. 1265 m., *Mexia 8834* (holotype in U. S. Nat. Herb.; isotypes in Gray Herb., Herb. Mo. Bot. Gard., and Herb. Univ. Calif.); mountains near Iguala, alt. 2500 ft., *Pringle 0228* (GH, MICH, US); Iguala Cañon, *Pringle 10060½* (GH, MICH, US); between Sochi and Tlalkinsala, alt. 3600–4800 ft., *Nelson 2036* (NY, US); Coyuca-Chacamerito, *Hinton 6621* (US). michoacán: Zitacuaro-La Mora, alt. 1325 m., *Hinton 13230* (GH).

There is a great superficial resemblance in the aspects of the flowering specimens of this species to those of *Heliocarpus occidentalis* Rose. It is, however, quite distinct from other species of *Triumfetta* and can easily be recognized.

Series Uncinatae Sprague & Hutch. in Jour. Linn. Soc. Bot. 39:240. 1909.

KEY TO THE SPECIES

A. Flowers hermaphrodite, the buds oblongoid, the style at least 3 times the length of the ovary; fruits distinctly pubescent.
  B. Petioles usually less than 1.5 cm. long, the leaves elliptical, at least twice as long as broad; southwestern Mexico.
    C. Fruit with more than 100 short, straight, glabrous spines, each about 1 mm. long; sepals at anthesis 13–16 mm. long; stamens 25–30 ..... 16. *T. brevipes*

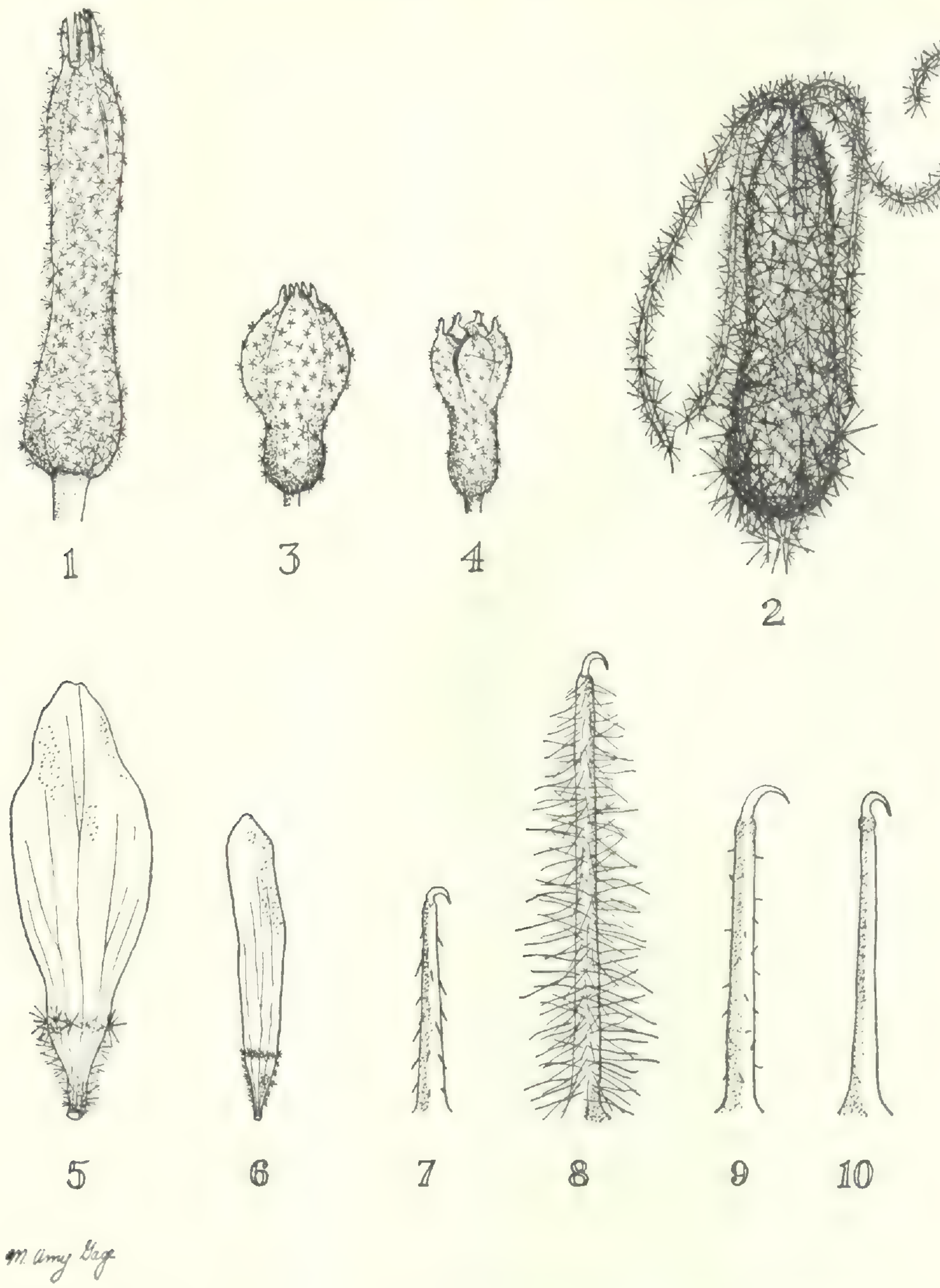

Fig. 7. Illustrations of taxonomic criteria for Series UNCINATAE:

1. Narrowly oblongoid floral bud of *T. Palmeri* with relatively short apical appendages.
2. Narrowly oblongoid floral bud of *T. Purpusii* with very long apical appendages.
3. Obovoid floral bud of *T. Galeottiana.*
4. Younger floral bud of *T. Bartramia* with very deeply cucullate sepals.
5. Broadly obovate petal of *T. bogotensis.*
6. Elliptical to narrowly obovate petal of *T. obscura.*
7. Retrorsely pilosulose spine of *T. semitriloba.*
8. Densely plumose spine of *T. socorrensis.*
9. Irregularly pubescent spine of *T. discolor* with few short hairs.
10. Glabrate spine of *T. paniculata.*

CC. Fruit with less than 75 falcate, pubescent spines, each about 2–3 mm. long; sepals at anthesis 15–20 mm. long; stamens 20.... 17. *T. Palmeri*

BB. Petioles generally much longer than 2.0 cm., the leaves ovate (except in *T. obscura*), usually much less than twice as long as broad.

C. Stamens 20–40 (except *T. Lappula* with 5–15); mature fruit (including spines) 7–15 mm. thick.

D. Spines plumose or irregularly pubescent; sepals at anthesis 1.2–3.0 cm. long.

E. Fruit body oblongoid with about 20 spines, each 6–10 mm. long; sepals at anthesis 12–14 mm. long; Revilla Gigedo Islands, Mexico..... 18. *T. socorrensis*

EE. Fruit body globose with 40 or more spines, each usually 2–5 mm. long; sepals at anthesis 1.5–3.0 cm. long.

F. Fruit with 40–50 spines; apical appendages of the sepals 5–10 mm. long; stamens about 40.

G. Spines densely plumose; apical appendages of the sepals 7–10 mm. long; southeastern Mexico..... 19. *T. Purpusii*

GG. Spines slightly pubescent to nearly glabrate; apical appendages of the sepals 5–7 mm. long; southwestern Mexico..... 20. *T. falcifera*

FF. Fruit with 75–200 spines; apical appendages of the sepals shorter than 3 mm.; stamens 15–30.

G. Leaves densely tomentose on both surfaces; mature fruit 6- to 10-loculate, each cell 1-seeded.

H. Mature fruit 8- or 10-loculate; sepals at anthesis 1.8–2.7 cm. long, the apical appendages 2–3 mm. long.

I. Mature fruit 5- to 10-loculate, the spines and body very shortly pubescent; sepals broadly obovate, the stamens 25–30; Peru..... 21. *T. multilocularis*

II. Mature fruit 8-loculate, the spines and body with long plumose hairs; sepals elliptical to narrowly obovate; stamens 20; Colombia..... 22. *T. mollissima*

HH. Mature fruit 6-loculate; sepals at anthesis about 1.7 cm. long, the apical appendages about 1 mm. long; northeastern Brazil..... 23. *T. longicoma*

GG. Leaves densely tomentose on lower surfaces only or both surfaces lightly pubescent to glabrescent; fruit with 3, 1- to 2-seeded locules.

H. Sepals at anthesis 22–30 mm. long; fruit indehiscent insofar as known.

I. Leaves 11–16 cm. long and 6–9 cm. wide, or slightly larger; fruit stellate-pubescent, spines briefly but distinctly pubescent.

J. Leaves 3-lobed, without tufts of hairs at axils of the veins on the lower surface; filaments lightly stellate-pubescent at the base; spines very lightly pubescent with short hairs; northwestern Mexico..... 24. *T. chihuahuensis*

JJ. Leaves not lobed, with many long tufts of hairs at the axils of the veins on the lower surface; filaments not pubescent; spines rather densely pubescent; west-central Mexico..... 25. *T. barbosa*

II. Leaves 6–8 cm. long and 3–4 cm. wide; fruit tomentose, the spines glabrescent; central and southwestern Mexico..... 26. *T. columnaris*

HH. Sepals at anthesis 15–20 mm. long; fruit easily dehiscent.

I. Leaves distinctly longer than broad, gradually and narrowly acuminate, both surfaces lightly pubescent to glabrescent; fruit with 100 or more slender spines, each about 4 mm. long; southern Mexico and West Indies to northern South America..... 27. *T. grandiflora*

II. Leaves nearly as broad as long, shortly acute to acuminate, tomentose beneath; fruit with about 75 relatively thick spines, each about 2–3 mm. long; northwestern Mexico..... 28. *T. discolor*

DD. Spines retrorsely pilosulose; sepals at anthesis 3–9 mm. long (except *T. bogotensis* and *T. abutiloides* sometimes up to 13 mm. long).

E. Petals present; fruit and flower with a 5-glandular gonophore, the urceolus manifest.

F. Leaves with both stellate and simple hairs, the latter prominent on both surfaces; sepals at anthesis 8–13 mm. long, the petals broadly obovate.

G. Leaves densely tomentose on both surfaces; apical appendages of the sepals nearly obsolete or less than 1 mm. long; fruit with 6, 1-seeded locules at maturity; Haiti and northern South America..... 29. *T. abutiloides*

GG. Leaves lightly pubescent on both surfaces; apical appendages of the sepals 2–3 mm. long; fruit with 3, 2-seeded locules at maturity; pantropical..... 30. *T. bogotensis*

FF. Leaves with stellate pubescence only; sepals at anthesis 5–9 mm. long, the petals linear to narrowly obovate.

G. Leaves and bracts narrowly elliptical, at least twice as long as broad; northeastern South America..... 31. *T. obscura*

GG. Leaves ovate, generally 3-lobed, less than twice as long as broad, the bracts elliptical.

H. Leaves slightly pubescent, glabrescent; petals less than half the length of the sepals; mature fruit body about 3 mm. thick; western Mexico..... 32. *T. acracantha*

HH. Leaves coarsely stellate-pubescent; petals subequalling the sepals; mature fruit body usually 4 mm. thick or more.

I. Petioles with 4 prominent glands on the basal sinus; mature fruit 8- to 10-loculate, the spines numerous, about 200; Trinidad and northern South America..... 33. *T. althaeoides*

II. Petioles without glands at the basal sinus; fruit 3-loculate, the spines 75 or fewer.

J. Apical appendages of the sepals 2 mm. long or less; fruit body lightly to densely pubescent, spines about 75; pantropical..... 34. *T. semitriloba*

JJ. Apical appendages of the sepals 3 mm. long or more; fruit body tomentose, the spines 25–40; Ecuador and Peru..... 35. *T. oligacantha*

EE. Petals absent; gonophore and urceolus obsolete in fruit and flower, the glands absent; pantropical..... 36. *T. Lappula*

CC. Stamens 5–15; mature fruit (including spines) 4–6 mm. thick.

D. Sepals very slightly cucullate in younger floral buds; fruit very lightly pubescent.

E. Leaves densely tomentose on both surfaces, 9–12 cm. long and 7–10 cm. wide; fruit with few, 50 or less, spines, each about 2 mm. long; Colombia and Ecuador..... 37. *T. sericata*

EE. Leaves lightly pubescent on both surfaces, glabrescent, about 2 cm. long and 1 cm. wide; fruit with numerous, 75–100 short spines, each about 1 mm. long or less; southwestern Mexico..... 38. *T. brachistacantha*

DD. Sepals cucullate about half their length in young floral buds; fruit densely pubescent.

E. Floral buds 5–8 mm. long slightly before anthesis, the urceolus manifest, the stamens 10–15; fruit body densely cinereous-tomentose, the spines glabrescent; West Indies and northern South America..... 39. *T. Bartramia*

EE. Floral buds 3–4 mm. long slightly before anthesis, the urceolus absent, the stamens 5; fruit body and spines densely plumose; northeastern Brazil..... 40. *T. Sampaioi*

AA. Flowers either hermaphrodite or pistillate, the hermaphroditic buds obovoid, the style about twice the length of the ovary; fruits essentially glabrous.
B. Leaves 15–18 cm. long and 16–20 cm. wide, 3- to 5-lobed; stamens 30–40; mature fruit body 5–6 mm. thick, the spines 3–5 mm. long; western Mexico..... 41. *T. paniculata*
BB. Leaves usually 7–15 cm. long and 5–12 cm. wide, not lobed to slightly 3-lobed; stamens 20–30 in hermaphroditic flowers, staminodial or absent in pistillate; mature fruit body 2–4 mm. thick.
C. Pistillate flower apetalous; (hermaphroditic floral bud 5–7 mm. long slightly before anthesis, the petals about 3–4 mm. long); fruit body 3–4 mm. thick, the spines 30–40; southern Mexico.... 42. *T. Galeottiana*
CC. Pistillate flower with petals, each about 1 mm. long; (hermaphroditic flower not seen); mature fruit body about 2 mm. thick, the spines about 20; central Mexico..... 43. *T. heliocarpoides*

16. Triumfetta brevipes S. Wats. in Proc. Am. Acad. 22:400. 1887. (T.: *E. Palmer 323*).

Spreading bushy shrubs 1–2 m. high; branches and inflorescence axes rough, scurfy, ferruginous-tomentose. Leaves broadly elliptical, about 11–13 cm. long and 3–4 cm. wide, the base obtuse, the tip gradually acuminate, the serrations unequal and blunt, usually glandular, the upper surface lightly but coarsely stellate-pubescent, the lower densely stellate-tomentose; petioles 1.0–1.5 cm. long, densely tomentose. Inflorescences axillary, the cymes of 2, rarely 3, cymules, generally condensed, the flowering peduncles 3–4 mm. long, the pedicels short, about 2 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 1.0–1.4 cm. long at anthesis, slightly constricted in the middle, the apical appendages slender, about 2–3 mm. long, slightly pubescent; sepals oblong, about 13–16 mm. long including the apical appendages, densely tomentose without, glabrescent within; petals narrowly obovate, about 10 mm. long, the claw about 4 mm. long, shortly plumose; gonophore about 1.5 mm. long and nearly as wide, the glands broadly oblong, 1.0–1.5 mm. long and 0.75–1.0 mm. wide; urceolus large, about 1 mm. high or more, indistinctly lobed, slightly ciliate; stamens 25–30, the filaments smooth, without serrations; ovary orbicular, about 1.5 mm. long, the spinules numerous, recurved, the style about 8–9 mm. long, the stigma acute. Fruit orbicular, the body about 6–7 mm. in diameter at maturity, matted cinereous-tomentose, 3-loculate, each cell 1-seeded, the spines numerous, 100 or more, straight, glabrous, each about 1 mm. long; seeds pyriform, 3.0–3.5 mm. long and 2.5–3.0 mm. wide.

A common ground cover in pine and oak forests or rocky hillsides at altitudes of 1000 m. or more in southwestern Mexico; flowering in August and September, the fruit maturing from late September to mid-October.

Mexico: guerrero: Tierras Blancas, Mina, alt. 1400 m., *Hinton 9922* (GH, US). jalisco: Río Blanco, *E. Palmer 323* (GH, US); rocky hills under oaks near Guadalajara, *Pringle 4502* (BR, GH, Mo, US); barranca of Río Blanco, near Guadalajara, alt. 4500 ft., *Pringle 11388* (GH, US); near Chapala, *Rose & Painter 7605* (GH, US). michoacan: road from Tancitaro to Apatzingan, alt. 3400 ft., *Leavenworth 1771* (Mo); vicinity of Morelia, Loma Sta. Maria, alt. 1950 m., *Arsène 2516* (K, Mo, P, US); vicinity of Morelia, vers la Huerta, alt. 1950 m., *Arsène 5131* (GH, Mo, US); vicinity of Morelia, alt. 1900 m., *Arsène 5546* (GH, Mo, US).

The shortly petiolate elliptic leaves, the orbicular fruit with numerous very short glabrous spines, and the oblongoid floral bud 10–14 mm. long at about anthesis, are characters which distinguish this species.

17. Triumfetta Palmeri S. Wats. in Proc. Am. Acad. 22:400. 1887. (T.: *E. Palmer 330*).

Low shrubs about 1 m. high; branches and inflorescence axes scurfy, ferruginous-tomentose. Leaves narrowly elliptic, about 6–8 cm. long and 2–3 cm. wide, the base obtuse, the tip gradually acuminate, the serrations rather regular and double, the upper surface lightly stellate-pubescent, the lower more densely so; petioles very short, not longer than 1 cm., densely tomentose, nearly obsolete in the bracts. Inflorescences axillary, the cymes usually of 3 cymules, rarely 4, each cymule 2-, rarely 3-flowered, the flowering peduncles variable in length, usually 4–6 mm. long, the pedicels about 2–3 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, 14–18 mm. long slightly before anthesis, usually falcate, the apical appendages short, slender, 1–2 mm. long, slightly pubescent; sepals narrowly ovate, about 15–20 mm. long including the apical appendages, densely tomentose without, glabrescent within; petals about 8–9 mm. long, narrowly obovate, with a claw about 2 mm. long, very densely plumose; gonophore slender, 1.0–1.5 mm. long, the glands oblong, about 1 mm. long and 0.5 mm. wide; urceolus very short, about 0.25 mm. high, rather obscurely 5-lobed, briefly ciliate; stamens 20, the filaments without serrations, slightly pubescent at the base; ovary orbicular, about 1 mm. long, the spinules numerous, recurved, the style 10–12 mm. long, the stigma acute. Fruit orbicular, the body about 4–5 mm. in diameter at maturity, with many short, stellate hairs, 3-loculate, each cell 1-seeded, the spines falcate, about 75, lightly pubescent to retrorsely pilosulose, 2–3 mm. long; seeds pyriform, about 3.0 mm. long and 2.5 mm. wide.

Southwestern Mexico, usually at altitudes of 1000–2000 m.; flowering in mid-August, and the fruit maturing from mid-September to early October.

Mexico: durango: Sierra Madre, *Rose 3510* (GH). jalisco: Río Blanco, *E. Palmer 330* (Mo, US); on the road between Colotlán and Bolaños, *Rose 2838* (US); Sierra Madre, west of Bolaños, *Rose 3701* (US); near Guadalajara, *Rose & Painter 7447* (US); barrancas near Guadalajara, *Pringle 4493* (BR, Mo, US); barranca near Río Blanco near Guadalajara, alt. 4500 ft., *Pringle 11389* (US).

This species is closely related to *T. brevipes*, but may be distinguished from the latter by its floral buds, which are 3–4 mm. longer at about anthesis, and also by its falcate, relatively longer, pubescent spines.

18. Triumfetta socorrensis T. S. Brandg. in Erythea 7:1. 1899. (T.: *Anthony 378*).

Handsome shrubs about 1.5–2.0 m. high; branches and inflorescence axes rough, scurfy, ferruginous-tomentose. Leaves broadly ovate to rhombic-ovate, about 5–6 cm. long and 4–5 cm. wide, the base rounded or cordate, the tip abruptly acuminate, the serrations very irregular, unequal and blunt, the upper surface coarsely stellate-tomentose, the lower more densely so; petioles about 2.0 cm. long, stout,

densely tomentose. Inflorescences axillary, the cymes of 3–4, very rarely 2, cymules, generally condensed, the flowering peduncles very short, 1–2 mm. long, the pedicels 2–3 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, about 9–11 mm. long slightly before anthesis, very slightly constricted near the base, the apical appendages short, about 1 mm. long; sepals broadly elliptical, about 12–13 mm. long at anthesis including the apical appendages, densely tomentose without, glabrescent and greenish within; petals broadly obovate, about 8–9 mm. long, the claw about 2–3 mm. long, densely plumose; gonophore short and stout, about 0.75 mm. long and 1.5 mm. thick, the glands small, spherical; urceolus short, about 0.5 mm. high, distinctly many-lobed, slightly ciliate; stamens about 20, the filaments glabrous; ovary orbicular, about 1.5 mm. long, the spinules about 30, recurved, the style about 3–4 times the length of the ovary, the stigma very briefly 2-fid. Fruit oblongoid, the body about 3–4 mm. in diameter and 5–6 mm. long at maturity, densely stellate-tomentose, 3-loculate, each cell 1-seeded, the spines about 15–20, 6–10 mm. long, densely pubescent with many short spreading hairs; seeds pyriform, 2.0–3.0 mm. long and 1.5–2.0 mm. wide.

Known only from Socorro Island adjacent to the mainland off the coast of Baja California, Mexico; flowering and fruiting from March to June.

Mexico: revilla gigedo islands: I. Socorro: *Anthony 378* (Mo, NY, UC, US); *Barkelew 107* (Mo, UC, US); Grayson's Cove, *Mason 1672* (Mo, US); dry slopes, north anchorage, *Howell 8444* (US).

A very distinct species and an endemic, it is conveniently recognizable by its densely tomentose, rhombic-ovate leaves with very short petioles, and also by its very characteristic oblongoid fruits with few densely plumose, long spines. In its vegetative and floral characters, it is closely related to *T. brevipes*, a common species of southwestern Mexico, and in its fruit characters to *T. Purpusii*, an endemic from Vera Cruz, Mexico.

19. Triumfetta Purpusii Standl. in Field Mus. Publ. Bot. 11:167. 1936. (T.: *Purpus 9009*).

Tall sparingly branched shrubs about 1.5 m. high; branches and inflorescence axes rough, scurfy, ferruginous-tomentose. Leaves broadly ovate, about 8–9 cm. long and 4–5 cm. wide, the base subcordate, the tip gradually and narrowly acuminate, the serrations unequal and blunt, generally glandular, the upper surface lightly stellate-pubescent, the lower densely tomentose; petioles 3–5 cm. long, densely stellate-pubescent. Inflorescences axillary, the cymes of 2, rarely 3, cymules, generally condensed, the flowering peduncles about 2–3 mm. long, the pedicels of about the same length. Flowers hermaphrodite, the buds broadly oblongoid, 8–12 mm. long slightly before anthesis, the apical appendages very slender, about 6–10 mm. long, usually reflexed upon the bud, densely plumose; sepals oblong, about 16–20 mm. long including the apical appendages, densely long-tomentose without, glabrescent within; petals obovate to narrowly so, about 6–8 mm. long, the claw about 4 mm. long, densely plumose; gonophore about 1.0 mm. long and 1.5–2.0 mm. wide, the glands large, oblong, 1.0–1.5 mm. long and 0.75–1.0 mm. wide;

urceolus small, about 0.5 mm. high, very deeply many-lobed, lightly ciliate; stamens about 40, the filaments smooth; ovary orbicular, about 1 mm. long, the spinules about 50, recurved, the style about 8–9 mm. long, the stigma acute. Fruit suborbicular, the body about 5 mm. wide, very densely tomentose, 3-loculate, each cell 1-seeded, the spines straight, about 40, each about 2 mm. long, with many long plumose hairs; seeds pyriform, 2.0–2.5 mm. long and 1.5–2.0 mm. wide.

Known only from Vera Cruz, Mexico. Flowers and fruits from November to March.

MEXICO: VERA CRUZ: Mata Zarza, *Purpus 9009* (FM, GH, Mo, NY, UC, US); barranca de Panoaya, *Purpus 8609* (GH, Mo, NY, UC, US); Baños de Azufre, *Purpus 8274* (GH, Mo, NY, UC, US); Remudatero, *Purpus 11099* (Mo, US).

The presence of very long appendages of the sepals makes *T. Purpusii* and *T. falcifera* very distinct from the rest of the species. This species can be distinguished from the latter, in flower by its calycine apical appendages, which are not only longer by about 2 mm. or more but are also more densely plumose; and in fruit, by the densely plumose body and the spines.

20. TRIUMFETTA FALCIFERA Rose, in Contr. U. S. Nat. Herb. 12:285. 1909. (T.: *E. Palmer 63*).

Bushy shrubs about 2 m. high; branches and inflorescence axes smooth with many long, spreading, stellate hairs. Leaves narrowly to broadly ovate, 12–15 cm. long and 6–9 cm. wide, the base obtuse to subcordate, the tip narrowly and gradually acuminate, the serrations rather regular, generally glandular, the upper surface lightly stellate-pubescent, the lower more densely and softly so; petioles 5–7 cm. long with long, spreading, stellate tomentum. Inflorescences generally axillary, sometimes terminal, the cymes of 1 cymule, the flowering peduncles about 8 mm. long and the pedicels about 6 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 6–10 mm. long at anthesis, the apical appendages very slender, 5–7 mm. long, usually spreading, rather densely plumose; sepals oblong, about 12–16 mm. long including the apical appendages, lightly long-plumose without, brownish and glabrescent within; petals obovate, about 3–4 mm. long, the claw about 1 mm. long, lightly plumose; gonophore about 1 mm. long, nearly 2 mm. wide, the glands narrowly elliptical; urceolus rather short, 0.25–0.5 mm. high, distinctly many-lobed, lightly ciliate; stamens about 40, the filaments glabrous; ovary orbicular, about 1.5 mm. long, the spinules about 40, recurved, the style 6–7 mm. long, the stigma acute, sometimes very briefly 2-fid. Fruit orbicular, about 4 mm. in diameter at maturity, very lightly pubescent, usually 3-loculate, sometimes 4- to 6-celled by false-septation, each cell 1-seeded, the spines about 40, straight, essentially glabrous, each about 2 mm. long; seeds pyriform, 2.0–2.5 mm. long and 1.5–2.0 mm. wide.

Southern Mexico; flowering and fruiting in September and October.

MEXICO: GUERRERO: in Acapulco and vicinity, *E. Palmer 63* (US), *266* (Mo, UC, US); Baqueta, alt. 200 m., *Langlassé 502* (P, US); Acapulco, presqu'iles Griffon, *Le Jolis s. n.* (G). TABASCO: Jalapa, Tequisatlán, *Liebmann 502* (US). DATA INCOMPLETE: *Liebmann 534A* (US).

21. Triumfetta multilocularis Hochr. in Ann. Conserv. Jard. Bot. Genève 18:104. 1914. (T.: *Pavon s. n.* in Herb. Genève).

Small trees or shrubs 2–4 m. high; branches and inflorescence axes rough, rather densely tomentose, with relatively long, ferruginous, stellate hairs. Leaves broadly ovate, usually 3-lobed, 8–10 cm. long and 6–7 cm. wide, cordate, narrowly and gradually acuminate, the serrations very irregular and rather large, not glandular, the upper surface coarsely stellate-pubescent, the lower more softly and densely so; petioles 4–6 cm. long, rather stout, with many spreading, long, stellate hairs. Inflorescences axillary, the cymes usually of 1, rarely 2, cymules, loose and spreading, the bracts usually broadly ovate, not lobed, the flowering peduncles 8–12 mm. long, the pedicels about 6 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 22–25 mm. long and 3–4 mm. wide slightly before anthesis, the apical appendages rather stout, 2–3 mm. long, lightly pubescent; sepals broadly obovate, about 27 mm. long including the apical appendages, stellate-pubescent without, glabrescent within; petals broadly obovate, showy, about 24 mm. long and 4–6 mm. wide, the claw about 4 mm. long, densely plumose; gonophore large, about 1.5–2.0 mm. long and wide, the glands quadrangular, large, about 1.5 mm. long and 1.0 mm. wide; urceolus 10-lobed, about 0.75 mm. high, distinctly ciliate; stamens 25–30, the filaments retrorsely 2-serrate, slightly pubescent at the base; ovary ovoid, 1.5–2.0 mm. long, the spines numerous, recurved, the style about 22 mm. long, pubescent at the base, the stigma acute. Fruit orbicular, the body about 6–8 mm. in diameter at maturity, lightly and briefly stellate-pubescent, 3- to 5-loculate, each cell 2-seeded, later falsely 8- to 10-loculate, each cell with 1 seed, the spines numerous, short, 1–2 mm. long, very shortly pubescent; seeds ovoid, about 2 mm. long and broad.

Peru; growing at altitudes of 2000–3000 m.; flowering and fruiting from June to December.

Peru: ayacucho: between Huanata and Río Apurimac, alt. 2200 m., *Killip & Smith 22300* (US). cuzco: San Miguel, Urubamba Valley, alt. 1800 m., *Cook & Gilbert 1126, 1163* (US); Prov. Quispicanchis, Dist. Marcapata, *Vargas 9685* (Mo); below Machu Picchu, lower valley slopes, alt. 2100 m., *West 6473* (Mo). huanuco: "Fl. de Huayaquil", *Pavon s. n.* (G); "Herbier de Ventenat", *s. n.* (G, FM photo); Acomayo, upon banks of Río Acomayo, alt. 2100 m., *Woytkowski 34013* (Mo). junin: Prov. Tarma, Carpapata, alt. 2400 m., *Ochoa 287* (US); Carpapata, above Huacapistana, alt. 2400 m., *Killip & Smith 24361* (US); Huacapistana, *Rose & Rose 18550* (NY, US); Prov. Tarma, between Palca and Carpapata, alt. 2900 m., *Stork 10970* (Mo). lima: Escuela Nac'l. Agric., from Prov. Sandia & Huacapistana and Tarma, *Mexia 4065* (Mo). data incomplete: Amazonian slope of the Andes, alt. 10,000–11,000 ft., *B. Eble s. n.* (NY).

Ornamental shrub or small tree with long whip-like branches. Though sufficiently distinct from *T. mollissima*, it is usually misidentified with it. The much larger flowers with broadly obovate, rather showy petals, and the pubescent to nearly glabrescent fruits, with numerous very short spines, clearly distinguish this species from the former.

22. TRIUMFETTA MOLLISSIMA HBK. Nov. Gen. & Sp. 5:345. 1821. (T.: "S. Fé de Bogota," *Bonpland s. n.* in Herb. Paris.).

Triumfetta acuminata HBK. loc. cit. 344. 1821. (T.: *Bonpland s. n.* in Herb. Paris.).

Shrubs about 1–2 m. high; branches and inflorescence axes rough, very densely long ferruginous-tomentose. Leaves broadly ovate to 3-lobed, 12–15 cm. long and 6–8 cm. wide, rounded or subcordate at the base, gradually and narrowly acuminate, the serrations very irregular, blunt and generally glandular, the upper surface scabrous, very pubescent, the lower smooth, densely tomentose; petioles 3–5 cm. long, rather stout, with long spreading ferruginous tomentum. Inflorescences axillary, the cymes of 2–3, rarely 1, cymules, rather lax, the bracts broadly lanceolate to elliptical, long-acuminate, the flowering peduncles about 8 mm. long, the pedicels about 6 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, 15–20 mm. long and about 2 mm. wide slightly before anthesis, the apical appendages slender, 1–2 mm. long, very lightly pubescent; sepals narrowly elliptical, 18–22 mm. long at anthesis, with many long spreading stellate hairs without, glabrescent within; petals linear, 16–18 mm. long, the claw 3–4 mm. long, densely plumose; gonophore rather large, about 1 mm. long and 1–2 mm. wide, the glands quadrangular, large, subequalling the gonophore; urceolus about 1 mm. high, distinctly 5-lobed, densely ciliate; stamens 20, the filaments slightly pubescent at the base, smooth; ovary orbicular, about 2 mm. long, the spinules numerous, recurved, the style 16–17 mm. long, the stigma acute. Fruit orbicular, the body 6–8 mm. in diameter at maturity, densely tomentose with long spreading hairs, 4-loculate, each cell 2-seeded, later falsely 8-loculate with 1 seed to a cell, the spines numerous, 100 or more, each 2–3 mm. long, long-plumose at the base; seeds ovoid, about 2 mm. long and broad.

Known only from Colombia; growing in dry open areas, at altitudes of 1200–2000 m.; flowering and fruiting from May to November.

COLOMBIA: ANTIOQUIA: vic. Medellin, *Toro 117, 501, 701* (NY); Dabeiba, *Johnson & Barkley 18c 676* (US); Bello, alt. 1500–1800 m., *Archer 218* (US). CALDAS: Supia, Cordillera Occidental, alt. 1200–1500 m., *Pennell 10710* (NY). CAUCA: forests in highlands of Popayán, alt. 1700–2000 m., *Lehmann 5521* (NY, US); Tolima, *Lehmann 2196* (G); Río Sucio to Río Piedras, west of Popayán, alt. 1500–1700 m., *Pennell & Killip 8227* (NY); La Manuelita, near Palmira, eastern side of Cauca Valley, alt. 1100–1300 m., *Pittier 818* (US); Municipio Popayán, alt. 1800 m., *Agredo 252* (US); El Tambo, Vertiente Oriental, alt. 1700 m., *Sneidern 4745, 5559, 5671* (US); Popayán, matorrales en Río Blanco, alt. 1800 m., *Arbelaez & Cuatrecasas 5761* (US); El Tambo, *Garcia B. 4418* (US). CUNDINAMARCA: Estacion Santana, arriba de Sasaima, alt. 1600–1700 m., *Dugand & Jaramillo 3845* (US); entre Pandi e Icononzo, alt. 980–1340 m., *Garcia B. 11095* (US); Villete, *Ariste-Joseph s. n., 5373* (US). DISTRITO FEDERAL: S. Fé de Bogota, *Bonpland s. n.* (P, Mo photo, NY); exact locality lacking, *Bonpland s. n.* (P, Mo photo). VALLE: Palmira, Cordillera Central, alt. 1200–1800 m., *Pennell & Killip 6101* (NY); Pichinde, bank of Río Cali, alt. 1600 m., *Duque 1474* (US); La Cumbre, Cordillera Occidental, alt. 1500–1700 m., *Pennell 5214* (US); Río Bolo, alt. 1000 m., *Dryander 253, 254* (US). DATA INCOMPLETE: *Triana 3230* (US); *Mutis 2788, 4171* (US); Piedra de Moler, *Holton 778* (NY); *Linden s. n.* (NY).

The reason for the discrepancy in the description of the leaf-shape of *T. acuminata* is very obviously due to the fact that the authors mistook the bracts for vegetative leaves. I have seen the types of both *T. mollissima* and *T. acuminata* and am convinced that they are conspecific. The type of *T. mollissima* has both the vegetative leaves and the bracts, while that of *T. acuminata* has only the bracts.

23. Triumfetta longicoma St. Hil. Fl. Bras. Merid. 1:221. 1825. (T.: *St. Hilaire B. 19*).

Older branches smooth, glabrescent, the younger ones and inflorescence axes longitudinally ridged, clothed with long stellate hairs. Leaves broadly ovate, about 8 cm. long and 4–6 cm. wide, cordate, narrowly and gradually long-acuminate, both surfaces with scattered tufts of long stellate hairs, especially on the veins; petioles 2–3 cm. long, slender, with few long stellate hairs. Inflorescences axillary, the cymes of 2–3 cymules, the flowering peduncles 3–4 mm. long, the pedicels 2–3 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, about 15 mm. long and 2–3 mm. wide slightly before anthesis, the apical appendages short, about 1 mm. long, glabrescent; sepals oblong, about 17 mm. long, densely pubescent without with long stellate hairs, glabrescent within; petals obovate, about 14 mm. long and 3 mm. wide, the claw about 2–3 mm. long, briefly ciliate; gonophore stout, about 1.0 mm. long and 1.5 mm. wide, the glands narrowly elliptical; urceolus deeply 5-lobed, about 0.5 mm. high, densely ciliate; stamens about 20, the filaments smooth, glabrous; ovary ovoid, about 1 mm. long, the spinules numerous, recurved, the style about 10 mm. long, the stigma acute. Fruit lightly stellate-pubescent, the body about 5 mm. in diameter at maturity, 3-loculate, each cell 2-seeded, later 6-celled each with 1 seed by false septation, the spines numerous, slender, each about 4 mm. long, lightly pubescent; seeds ovoid, about 2 mm. long and broad.

Apparently a rare species of northeastern Brazil, usually growing along streambanks in wooded areas at altitudes of about 1000 m.; flowering and fruiting from May to July.

Brazil: minas gerais: Cobras, *St. Hilaire B. 19* (P, FM photo, US); Distr. Diamantina, Christais, near Corriga Duas Pontes, alt. 1160 m., *Mexia 5821* (NY, US). data incomplete: *Allemao & Sysneiros 1491* (R).

The characters that help in the identification of this species are the long golden-brown silky stellate tomentum, which clothes the younger branches, the inflorescence axes, the outside of the sepals, the leaves and the petioles, the relatively large flowers, and the comparatively long but weak spines. It is quite likely that *T. longicoma* is conspecific with the Old World *T. velutina* Vahl. I have not seen the type of the latter, but have seen a specimen from India in Hooker's Herbarium at Kew, labelled *T. velutina,* which matches well *T. longicoma.*

24. Triumfetta chihuahuensis Standl. in Contr. U. S. Nat. Herb. 23:744. 1923. (T.: *M. E. Jones s. n.* in U. S. Nat. Herb.).

Slender spreading shrubs 1–2 m. high; older branches lightly pubescent to

Fig. 8. *Triumfetta chihuahuensis*

nearly glabrate, punctate with prominent white lenticels, the younger stems and inflorescence axes densely pubescent with short stellate and simple hairs. Leaves broadly ovate, generally 3-lobed, 11–14 cm. long and 6–9 cm. wide, distinctly cordate, the middle lobes narrowly and gradually acuminate, the laterals acute to shortly acuminate, both surfaces nearly glabrous, only the primary veins lightly pubescent; petioles slender, 6–7 cm. long, briefly stellate-pubescent. Inflorescences axillary, the cymes of 2–3 cymules, usually opposite the bracts, the flowering peduncles about 5 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, showy, the buds broadly oblongoid, 24–26 mm. long and 3–4 mm. wide slightly before anthesis, the apical appendages about 1 mm. long, glabrescent; sepals oblong, 25–30 mm. long including the apical appendages, scattered stellate-pubescent without, glabrescent within; petals broadly obovate, 20–22 mm. long and 4–5 mm. wide, the claw about 3–5 mm. long, densely but very briefly pubescent; gonophore large, about 2.5 mm. long and 1.5 mm. wide, the glands oblong, about 2 mm. long and 1 mm. wide; urceolus short, distinctly many-lobed, briefly ciliate; stamens 20, the filaments smooth, lightly stellate-pubescent at the base; ovary orbicular, about 2 mm. long, the spinules numerous, recurved, the style about 22 mm. long, the stigma very briefly 3-parted. Fruit orbicular, the body about 6 mm. in diameter at maturity, very lightly stellate-pubescent, 3-loculate, each cell 1-seeded, the gonophore and glands prominent, the spines about 75–100, lightly pubescent with few scattered hairs; seeds ovoid, about 3.5 mm. long and 3.0 mm. wide.

Known only from southwestern Mexico, where it grows along steep, moist, shady canyons in pine forests at altitudes of 1000–1500 m.; flowers and fruits in September and October.

Mexico: chihuahua: Guayanopa Canyon, Sierra Madre Mts., alt. 5000 ft., *M. E. Jones s. n.* (Mo, US); near Batopilas, alt. 5500–6500 ft., *Goldman 211* (GH, US); Arroyo Hondo, Sierra Charuco, *Gentry 1780* (Mo, US). sinaloa: Ocurahui, Sierra Surotato, alt. 6000–7000 ft., *Gentry 6240* (Mo). sonora: Sanguaribo, Río Mayo, alt. 5500 ft., *Gentry 2123* (Mo, US).

This species is rather closely related to *T. columnaris*, but may be distinguished from it by the larger, usually 3-lobed leaves and also by the pubescent spines.

25. Triumfetta **barbosa** Ko Ko Lay, sp. nov.

Frutex circiter 2–4 m. altus. Ramuli graciles longitudinaliter sulcati 4-angulati glabrescentes. Folia late ovata non-lobata 14–16 cm. longa 7–10 cm. lata base cuneata vel rotundata apice longe attenuata subdupliciter serrata pilis sparse stellatis mox glabrescentia infra breviter stellato-pubescentia, in axillis nervorum dense longi-pubescentia. Inflorescentiae axillares, cymis cymulis 2, pedunculis circiter 4 mm. longis, pedicellis 8–10 mm. longis. Flores hermaphroditi, alabastro maturo oblongoideo 18–20 mm. longo; sepalis ellipticis 20–22 mm. longis extra breviter pubescentibus, appendiculis circiter 2 mm. longis glabris; petalis ellipticis vel obovatis 14–16 mm. longis, unguilo 2–3 mm. longo dense plumoso; gonophoro circiter 1.5 mm. longo, glandulis ellipticis 0.75–1.0 mm. longis; urceolo circiter 0.75 mm. alto, 5-lobato breviter ciliato; staminibus 20, filamentis usque ad 12–14

Fig. 9. *Triumfetta barbosa*

mm. longis glabris; ovario globoso circiter 1.5 mm. longo, spinulis 75–100 recurvatis, stylo glabro 15–16 mm. longo, stigmate acuto. Fructus globosus non dehiscens, corpore ipso 4–6 mm. diametro, breviter stellato-pubescens 3-locularis, loculis 1-spermis, aculeis circiter 75, 3–4 mm. longis breviter pubescentibus; seminibus ovoideo-acutis circiter 2 mm. longis et latis.

West-central Mexico.

MEXICO: JALISCO: Sierra Madre Occidental, Real Alto, trail to Arroyo del Jaguay, alt. 2500 m., *Mexia 1753* (holotype in Herb. Mo. Bot. Gard.; isotypes in Herb. Univ. Mich. and U. S. Nat. Herb.).

A species rather closely allied to *T. chihuahuensis*, but may be distinguished by its undivided long-attenuate leaves with dense tufts of hairs in the axils of the veins on the lower surface, and also by its more densely pubescent spines and glabrous filaments.

26. TRIUMFETTA COLUMNARIS Hochr. in Ann. Conserv. Jard. Bot. Genève 18:111. 1914. (T.: *Hartweg 448*).

Triumfetta pseudocolumnaris Hochr. loc. cit. 103. 1914. (T.: *Galeotti 4151*).
Triumfetta columnarioides Bullock, in Kew Bull. 292. 1937. (T.: *Hinton 4917*).

Shrubs about 2 m. high; older branches glabrescent, longitudinally ridged, the younger ones and inflorescence axes scurfy, with long spreading stellate and simple hairs. Leaves broadly ovate to obscurely 3-lobed, usually small, 6–8 cm. long and 3–4 cm. wide, rounded or subcordate at the base, gradually and narrowly long-acuminate, both surfaces lightly stellate-pubescent, slightly more so on the veins; petioles relatively stout, about 2–3 mm. long, coarsely long stellate-pubescent. Inflorescences axillary, the cymes of 2 cymules, usually opposite the bracts, the flowering peduncles 4–6 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 22–25 mm. long and about 3 mm. wide slightly before anthesis, the apical appendages slender, 1–2 mm. long, glabrescent; sepals oblong, about 25 mm. long including the apical appendages, glabrescent and brownish without, light yellow within; petals narrowly obovate, about 18 mm. long and 3–4 mm. wide, the claw 4–5 mm. wide, densely but briefly ciliate; gonophore large, about 2 mm. long and 1 mm. wide, the glands oblong; urceolus about 0.5 mm. high, 5-lobed, briefly ciliate; stamens 20, the filaments smooth, long stellate-pubescent at the base; ovary orbicular, about 2 mm. long, the spines numerous, recurved, the stigma very briefly 3-parted. Fruit orbicular, the body about 6 mm. in diameter at maturity, lightly stellate-pubescent, 3-loculate, each 1-seeded, the spines about 75–100, each 1–2 mm. long, lightly pubescent to nearly glabrate, the gonophore and glands prominent; seeds ovoid, about 2.5 mm. long and 1.5–2.0 mm. wide.

Central and southwestern Mexico, usually growing in oak forests, at altitudes of 1500–2500 m.; flowering and fruiting from October to December.

MEXICO: GUERRERO: Mina, Fresnos, alt. 2160 m., *Hinton 9749* (GH, US); Río Frio Diamentes, Mina, *Hinton 10734* (GH, Mo, US). MÉXICO: Comunidad, Temascaltépec, alt. 2350 m., *Hinton 4891* (GH, K, Mo, US), alt. 2300 m., *4917* (Mo, US). MICHOACAN: Sierra Terricillia, Coalcomán, alt. 2420 m., *Hinton 12349, 15144, 15270* (GH). MORELOS: Cuernavaca, *Holway 532* (NY). OAXACA: Cordillera, alt. 5000–6000 ped., *Galeotti 4151* (BR, FM photo); Tokontepeque (Tehuantepec?), *Hartweg 448* (NY, FM photo); "les montagnes ombragier en terre tempiric," *Ghiesbreght 175* (P).

The small leaves and large flowers tend to confuse this species with *T. Goldmani,* when examined superficially.

27. TRIUMFETTA GRANDIFLORA Vahl, Eclog. Amer. 2:34. 1796. (T.: *Ryan s. n.* in Herb. Copenhagen).

Triumfetta nemoralis St. Hil. Fl. Bras. Merid. 1:221. 1825. (T.: *St. Hilaire B. 1. 1070* in Herb, Paris.).
Triumfetta longiseta DC. Pl. Rar. Jard. Genève, 64. 1829. (T.: *Burat s. n.* "Havanne" in Herb. Deless.).
Triumfetta longicuspis Turcz. in Bull. Soc. Nat. Moscou 31[1]:229. 1858. (T.: *Jörgensen 882*).
Triumfetta cymosa Tr. & Planch. in Ann. Sci. Nat. Bot. IV, 17:353. 1862. (T.: "Quindio," *Triana s. n.* in Herb. Paris.).
Triumfetta cymosa var. *glabrescens* Tr. & Planch. loc. cit. 354. 1862.
Triumfetta cymosa var. *hirsuta* Tr. & Planch. loc. cit. 354. 1862. (T.: "Pampalona," *Triana s. n.* in Herb. Paris.).
Triumfetta grandiflora var. *brasiliensis* Hochr. in Ann. Conserv. Jard. Bot. Genève 18:100. 1914. (T.: *Glaziou 9356*).
Triumfetta boyacana Moldenke, in Phytologia 1:10. 1933. (T.: *Lawrance 7*).
Triumfetta Schunkei Macbr. in Candollea 5:381. 1934. (T.: *Schunke 1597*).

Shrubs 1–2 m. high; older branches glabrous, smooth, punctate with small white lenticels, the younger stems and inflorescence axes rough, generally clothed with many long stellate and simple hairs. Leaves broadly ovate, usually about 14 cm. long and 9 cm. wide, sometimes slightly larger, rounded or cuneate at the base, narrowly and gradually long-acuminate, both surfaces glabrescent or lightly scabrous with short stellate hairs, especially on the nerves; petioles slender, about 6–10 cm. long, usually lightly stellate-pubescent. Inflorescences terminal, the cymes of 1–2 cymules, usually opposite the bracts, the flowering peduncles about 6 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 14–18 mm. long and 3–4 mm. wide slightly before anthesis, the apical appendages slender, 1–2 mm. long, glabrescent; sepals linear-ovate, 15–20 mm. long including the apical appendages, glabrescent or lightly ferruginous-pubescent without; petals lanceolate to narrowly obovate, subequalling the sepals, the claw 3–5 mm. long, densely plumose; gonophore about 1.5 mm. long and 2.0 mm. wide, the glands spherical; urceolus about 0.5 mm. high, many-lobed, briefly ciliate; stamens 20, the filaments glabrous, smooth; ovary orbicular, about 2 mm. long, the spinules numerous, recurved, the style 14–16 mm. long, the stigma very briefly 3-parted. Fruit lightly pubescent, the body 5–6 mm. in diameter at maturity, rather easily loculicidally dehiscent, 3-loculate, each cell 2-seeded, the spines numerous, about 200, slender, 4–5 mm. long, lightly pubescent at the base, sometimes with few plumose hairs; seeds pyriform, glabrous, about 2–3 mm. long and 1.5–2.5 mm. wide.

Rather widely distributed throughout the American tropics, though not abundant at any single locality, usually growing at altitudes of about 1000 m.; flowering and fruiting in its northern range from September to December, and in its southern range from March to June.

MEXICO: OAXACA: Sierra San Pedro Nolasco, Talea, *Jörgensen 882, 960* (G); Chinantla, *Galeotti 4162A* (BR, NY, US). VERA CRUZ: Sierra Madre Misantla, *Purpus 6009* (UC).
GUATEMALA: ALTA VERAPAZ: Coban, alt. 1350 m., *Tuerckheim II 861* (BR, GH, Mo), alt. 4300 pp., *Tuerckheim 342* GH).

Panama: chiriquí: vicinity of El Valle de Antón, *Allen 2072* (Mo).
Cuba: havana: près de la Havana, *M. Santos-Burat s. n.* (P, Mo photo).
Martinique: *Sieber 79* (Mo); *Duss 2318* (Mo, NY).
Colombia: boyaca: region of Mt. Chapon, northwest of Bogotá, *Lawrance 7* (NY, US). santander: Eastern Cordillera, between El Roble and Tona, *Killip & Smith 19399* (US).
Brazil: minas gerais: Ponte dos Paulistas, Comarca do Cerro do Frio, *St. Hilaire B. I. 1070* (P); Belo Horizonte, *Barreto 7923* (R). rio de janeiro: Serra de Estrella près de Botequin, *Glaziou 9356* (BR, G); environs de Rio de Janeiro, *Glaziou 17470* (G). data incomplete: *Ryan s. n.* (C, FM photo).
Ecuador: pichincha: Puente Gloria de María, west of Quito, alt. 1200 m., *Asplund 7250* (US).
Peru: junin: Chanchamayo Valley, alt. 1500 m., *Schunke 1597* (FM). puno: Sandia, alt. 2100–2300 m., *Weberbauer 507, 508* (G). data incomplete: *Poeppig 2053* (FM photo).
Bolivia: cochabamba: Incachaca-S. Antonio, alt. 1500 m., *Werdermann 2127* (Mo). la paz: Prov. South Yungas, Bassin Río Bopi, San Bartolomé, near Calisaya, alt. 750–900 m., *Krukoff 10246* (Mo); Mapiri, *Bang 1490* (Mo, US); Achiquin, between Mapiri and Apolo, alt. 750 m., *Cardenas 1110* (NY); San Carlos, Mapiri, *Buchtien 1823* (US). tipuani: Hacienda Casana, *Buchtien 7368* (US).

The best single character for the identification of this species is its fruits, which are usually rather easily dehiscent at maturity and have numerous, very long slender spines. In flower, it may be recognized by its broadly oblongoid floral buds, which are about 14–18 mm. long and 3 mm. wide at about anthesis. The leaves are broadly ovate and the base is never cordate. There is considerable variation in the pubescence of the leaves; in general, though not always, plants from South America tend to be more pubescent than those from North America.

28. Triumfetta discolor Rose, in Contr. U. S. Nat. Herb. 12:285. 1909. (T.: *Rose 1979*).

Triumfetta dehiscens Rose, loc. cit. 285. 1909. (T.: *Rose 1698*).

Low, spreading, bushy shrubs about 8 dm. high; branches and inflorescence axes rough, scurfy, with many long, spreading, stellate hairs. Leaves broadly ovate to rhombic-ovate, about 7–9 cm. long and 6–8 cm. wide, the base rounded, rarely subcordate, the tip abruptly acute, the serrations unequal, blunt and irregular, the upper surface greenish, with few scattered, short, coarse, stellate hairs, the lower pallid, smooth, with dense stellate tomentum; petioles 3–5 cm. long, clothed with long, spreading, stellate hairs. Inflorescences axillary, rarely terminal, the cymes of 2 cymules, rather lax, the flowering peduncles 3–4 mm. long, the pedicels about 2 mm. long, the subtending bracteoles prominent. Flowers hermaphrodite, the buds oblongoid, about 15–20 mm. long slightly before anthesis, the apical appendages short, about 1 mm. long, lightly pubescent; sepals oblong, about 18 mm. long, brownish and lightly pubescent without, greenish and glabrescent within; petals broadly obovate, about 15 mm. long and 3–4 mm. wide, deep yellow, the claw about 2–3 mm. long, slightly plumose; gonophore broad, about 1 mm. long and 2–3 mm. wide, the glands quadrangular, subequalling the gono-

phore; urceolus prominent, about 0.75 mm. high, many-lobed, densely ciliate; stamens usually 20, rarely 25, the filaments glabrous; ovary orbicular, about 2 mm. long, the spinules numerous, recurved, the style 15–17 mm. long, the stigma acute. Fruit orbicular, the body about 6–7 mm. in diameter at maturity, slightly stellate-pubescent, loculicidally dehiscent, 3-loculate, each cell 2-seeded; spines about 75, about 2 mm. long, lightly pubescent; seeds ovoid, about 1.5–2.0 mm. long and 1.0–1.5 mm. wide.

Western Mexico, usually growing on rocky shaded slopes under oaks or in oak-savannahs at altitudes of 1000–1700 m.; flowering and fruiting from July to September.

MEXICO: DURANGO: Huasemote, *Rose & Hough 3503* (GH, US); along trail from Pueblo Nuevo to Cueva, Sierra Madre Occidental, alt. 1500–1700 m., *Harvey 18486* (US); exact locality lacking, *Rose 2255* (US). JALISCO: in the foothills of Sierra Madre, near Colomos, *Rose 1698* (GH, US). NAYARIT: in the foothills of Sierra Madre, Terr. de Tépic, between Pedro Paulo and San Blascito, *Rose 1979* (GH). SINALOA: Cerro Colorado, alt. 2500 ft., *Gentry 5127* (GH, Mo); Las Mesas, Sierra Surotato, alt. 3000 ft., *Gentry 6150* (GH, Mo), *6151* (Mo, US), *6151a* (Mo); Quebrado de Mansana, Sierra Surotato, alt. 4000–4500 ft., *Gentry 6526a* (GH, Mo); Las Mesas, Sierra Surotato, alt. 3000 ft., *Gentry 6652* (GH, Mo). SONORA: Sierra de Alamos, vicinity of Alamos, *Rose, Standley & Russell 12881* (NY, US).

The lightly stellate, easily dehiscent fruits, the large showy flowers, and the rhombic-ovate leaves with dense tomentum on lower surfaces, characterize this species.

29. TRIUMFETTA ABUTILOIDES St. Hil. Fl. Bras. Merid. 1:223. 1825. (T.: *St. Hilaire s. n.*, "Itajuru de San Miguel de Mato Dentro" in Herb. Paris.).

Sparsely branched, more or less trailing shrubs 1–3 m. high; older branches terete, scurfy, rather densely pubescent with long stellate and simple, frequently gland-tipped hairs, the younger ones and inflorescence axes very densely tomentose with long, spreading, stellate and simple hairs. Leaves broadly ovate, markedly 3-lobate, the lobes usually above the middle of the lamina, 12–14 cm. long and 8–10 cm. wide, the base subcordate, the terminal lobe long-acuminate, the laterals usually blunt, very rarely short-acuminate, the serrations very irregular, the basal ones always glandular, both surfaces densely pubescent with both stellate and simple hairs, the veins densely tomentose, the lower ones very prominent; petioles 3–4 mm. long, stout, densely long-tomentose, usually flattened and forming a callus at the sinus. Inflorescences on terminal branches, the cymes of 3 cymules, always in the axils of the bracts, rather lax, the bracts elliptical, the flowering peduncles about 3 mm. long, the pedicels 3–4 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, about 8–11 mm. long slightly before anthesis, the apical appendages about 1 mm. long; sepals oblong, 8–11 mm. long, grayish and rather densely tomentose without, yellow-brown and glabrescent within; petals subequalling the sepals, broadly obovate, showy, 7–10 mm. long and about 3 mm. wide, the claw 2–3 mm. long, densely plumose; gonophore slender, about 0.5 mm. long, the glands spherical to oblong, subequalling the gonophore; urceolus short,

about 0.5 mm. high, distinctly 5-lobed, densely ciliate; stamens 20, the filaments retrorsely 4-serrate; ovary orbicular, about 1.5 mm. high, the spinules numerous, recurved, the style 5–6 mm. long, the stigma briefly 3-parted. Fruit spheroid, the body rather densely pubescent, 3–5 mm. in diameter at maturity, 3-loculate, each cell with 2 seeds, on maturity with 6 definite 1-seeded locules, the spines 100 or more, each about 3 mm. long, retrorsely pilosulose; seeds lenticular, about 2 mm. long and wide, the funicular groove prominent.

A rather common widespread species of South America, with a few scattered representatives in the West Indies; commonly found in abandoned fields or as a roadside weed at altitudes from about 300 to 1500 m.; flowers and fruits from January to April.

HAITI: Massif de la Selle, Port-au-Prince, alt. 300 m., *Ekman 7213* (S), *7407* (S).

COLOMBIA: CAUCA: Las Suntas, alt. 300–500 m., *Lehmann 234* (G). MAGDALENA: Santa Marta, *H. H. Smith 1689* (NY, US).

VENEZUELA: DISTRITO FEDERAL: in valley, on road from El Valle to Cua, *Pittier 11974* (G); between Cotiza and Los Venados, near Caracas, *Allart 21* (US); Caracas and vicinity, *Bailey & Bailey 257* (US).

BRAZIL: MINAS GERAIS: Caldas, *Regnell I. 102* (S, US); Dist. Carangola, Fazenda da Gramma, about 6 km. north, *Mexia 4324* (Mo, US); Caldas, in campo, *Lindberg 284b* (BR, S); Itajuru de San Miguel de Mato Dentro, *St. Hilaire s. n.* (P); Passa Quatro, *Sampaio 6033, 6118* (R); Domingos Pisoni, Municipio de Leopoldini, *Barreto 7928* (R); Jard. Bot. de Belo Horizonte, *Barreto 7922* (R); exact locality lacking, *Claussen 482* (BR). RIO DE JANEIRO: Nova Friburgo, alt. 900 m., *Holway & Holway 1459* (US). RIO GRANDE DO SUL: Tristeza, Porto Alegro, *Malme 1404* (S); Canôas, Prov. Porto Alegro, *Malme s. n.* (S); Cascate, Prov. Gloria, *Malme 1353* (S). SÃO PAULO: Carapicho, *Mosén 1132* (S). SANTA CATHARINA: *Ule 813* (US). DATÁ INCOMPLETE: *Burchell 2491* (P).

ECUADOR: GUAYAS: Milagro, alt. 500 m., *Hitchcock 19960, 20240* (US). MANABI: Portoviejo, *Rose & Rose 23409* (US).

PERU: CUZCO: Prov. Quispicanchis, Tio, Marcapata, alt. 2000 m., *Vargas C. 3079* (Mo); Torontoy, Urubamba Valley, alt. 2400 m., *Cook & Gilbert 819* (US); Santa Ana, alt. 900 m., *Cook & Gilbert 1437* (US). HUANUCO: Huanuco, *Macbride 3521* (US); *Macbride & Featherstone 2053* (US). LORETO: Mishuyacu, near Iquitos, alt. 1000 m., *Killip & Smith 29894* (US). DATA INCOMPLETE: *Grisar s. n.* (P).

BOLIVIA: LA PAZ: Mapiri, alt. 2500 ft., *Rusby 1450* (US); Hacienda Simao sobre el camino a Tipuani, alt. 1400 m., *Buchtien 5452* (Mo, S, US), *5453, 5454* (US); Caranaim, Tipuani, *Buchtien 7367* (S, US); Nord Yungas, Milluguaya, alt. 1300 m., *Buchtien 788* (FM, Mo, S, US); Sirupaya bei Yanacachi, alt. 2100 m., *Buchtien 509* (US), *510* (S); Villa Aspiazu, *Holway & Holway 688* (US).

PARAGUAY: L'Asuncion, *Balansa 2327* (P).

ARGENTINA: FORMOSA: Riocho de Oro, *Reales s. n.* (Mo). MISIONES: Candelaria, Santa Ana, *Schwindt 49* (Mo); Posadas, *Ekman 199* (S, US). TUCUMÁN: Tafi, alt. 600 m., *Venturi 1767* (US).

This species is very closely related to *T. bogotensis*, with which it is often confused. It may, however, conveniently be distinguished from the latter by the very densely pubescent leaves, the short apical appendages of the sepals, and also by the presence of false septa in the fruit, which on maturity becomes completely 6-loculate, each with one seed.

30. TRIUMFETTA BOGOTENSIS DC. Prod. 1:506. 1824. (Based on *T. pilosa* HBK.).

Triumfetta pilosa HBK. Nov. Gen. & Sp. 5:343. 1821, non Roth (T.: *Bonpland s. n.* in Herb. Paris.).

Triumfetta sepium St. Hil. Fl. Bras. Merid. 1:22. 1825. (T.: *St. Hilaire Al. 156*).
Triumfetta dumetorum Schlecht. in Linnaea 11:377. 1837. (T.: *Keerl s. n.* in Herb. Brux.).
Triumfetta hispida A. Rich. in Sagra, Hist. Nat. Cuba 10:204. 1839. (T.: *de la Sagra s. n.* in Herb. Paris.).
Triumfetta grossulariaefolia A. Rich. loc. cit. 205. 1839. (T.: *de la Sagra s. n.* in Herb. Paris.).
Triumfetta Lindeniana Turcz. in Bull. Soc. Nat. Moscou 31^1:229. 1858. (T.: *Linden 59*).
Triumfetta Botteriana Turcz. loc. cit. 32^1:260. 1859. (T.: *Botteri 773*).
Triumfetta Orizaba Turcz. loc. cit. 261. 1859. (T.: *Botteri 771*).
Triumfetta Josefina Polak. in Linnaea 41:552. 1877. (T.: *Polakowsky 523*).
Triumfetta vincentina Urb. Symb. Ant. 5:414. 1908. (T.: *H. H. & G. W. Smith 1057*).
Triumfetta valenciensis R. Kunth, in Fedde's Rep. Sp. Nov. Beih. 43:464. 1927. (T.: *Pittier 8677*).
Triumfetta panamensis I. M. Johnston, in Sargentia 8:194. 1949. (T.:*Johnston 1112*).

Shrubs about 1–2 m. high; branches and inflorescence axes with many long, spreading hairs. Leaves broadly ovate, usually 3-lobed, 9–10 cm. long and 7–8 cm. wide, the base rounded to subcordate, the tip acuminate, the serrations very irregular, unequal and blunt, both surfaces lightly pubescent with both stellate and simple hairs, the latter prominent, long, either spreading or appressed; petioles about 4–6 cm. long, much shorter in the bracts, very densely tomentose with long simple and stellate hairs. Inflorescences axillary, the cymes of 2 or 3 cymules, the bracts broadly elliptical, the subtending bracteoles prominent, the flowering peduncles 4–7 mm. long, the pedicels 3–4 mm. long. Flowers hermaphrodite, the buds oblongoid, 7–11 mm. long slightly before anthesis, constricted about the middle, the apical appendages slender, 2–3 mm. long, lightly pubescent; sepals oblong, 8–13 mm. long including the appendages, long-hirsute without, glabrescent within; petals broadly obovate, about 8–9 mm. long and 3–4 mm. wide, the claw about 2 mm. long, densely plumose; gonophore slender, about 1 mm. long and 0.5 mm. wide, the glands elliptical, subequalling the gonophore; urceolus short, 0.25–0.50 mm. high, not lobed, distinctly ciliate; stamens 25–30, the filaments glabrous, without serrations; ovary suborbicular, about 1.5 mm. long, the spinules numerous, recurved, the style 8–9 mm. long, the stigma acute. Fruit spheroid, the body about 3–4 mm. in diameter at maturity, 3-loculate, each cell 2-seeded, the spines slender, about 75, retrorsely pilosulose, about 3 mm. long; seeds lenticular, 2–3 mm. long and about 2 mm. wide.

A widespread weedy species of tropical America, which grows in waste lands, cut-over forest areas, and on hill-slopes, up to an altitude of about 2000 m.; flowering and fruiting from late July to early December in its northern range, from October to January in its middle, and from November to April in its southern range.

The appressed simple hairs on both surfaces of the leaves, the broadly obovate petals, and the densely pilosulose spines distinguish this species from *T. semitriloba*.

MEXICO: GUERRERO: Galeana, Carrizo to Pie de la Cuesta, *Hinton 14735* (MICH). JALISCO: Atoyac, *Kerber 135* (G). MÉXICO: Temascaltépec, Bejucos, alt. 610 m., *Hinton 2021* (K). MICHOACAN: Cordillera, alt. 3000 ped., *Galeotti 4156* (BR, P); exact locality

lacking, *Galeotti 4053* (BR, P). OAXACA: near Etla, *Pringle 5718* (MICH); exact locality lacking, alt. 1750 m., *Conzatti & Gonzalez 1054* (GH); *Liebmann 515* (US). TAMAULIPAS: Río de la Ternera, *Purpus 8277* (NY, UC, US); Tampico, *Berlandier 71* (G, FM photo). VERA CRUZ: Jalapa, *F. W. Johnson s. n.* (NY); Jalapa, *Linden s. n.* (K), *59* (G, FM photo), *771* (G, K, P, FM photo, Mo), *772* (P), *773* (K, P, FM photo); Orizaba and vicinity, *Botteri 1089* (US), *Bourgeau 2846* (BR, G, P), *Müller 1600* (BR); Zacuapan, *Galeotti 7040* (BR). YUCATAN: Izamal, *Gaumer 001*, *1005* (BR, Mo), *1440* (Mo); Temax, *Gaumer 2130* (Mo); Calotmul, *Gaumer 2131* (BR); Chichankanab, *Gaumer 2035* (Mo); Xnocac, *Gaumer 23469* (Mo). DATA INCOMPLETE: *Linden 79* (BR), *211* (BR); *Hahn 65, 66* (P); *Keerl s. n.* (P).

BRITISH HONDURAS: exact locality lacking, *Peck 240* (K).

GUATEMALA: ALTA VERAPAZ: Cobán, alt. 1350 m., *Tuerckheim II 1957* (BR, Mo), alt. 4300 pp., *Tuerckheim 1359* (Mo); Samac to Chamá, alt. 2500 ft., *H. Johnson 781* (US). DATA INCOMPLETE: *Savage s. n.* (P).

NICARAGUA: SEGOVIA: environ de Granade, alt. 40 m., *Lévy 380* (G, P).

COSTA RICA: ALAJUELA: collins de San Pedro en San Ramon, alt. 1050–1075 m., *Brenes 601* (FM). CARTAGO: northwest slope of Cerro Carpintera, above La Unión, Tres Ríos, alt. 1320–1500 m., *Dodge & Thomas 4828* (Mo). GUANACASTE: defrichements sur les bords du Tiliri, *Tonduz 7208* (BR, GH). HEREDIA: Vera Blanca de Sarapiqui, between Poas and Barba volcanoes, alt. 1710 m., *Skutch 3374* (Mo). SAN JOSÉ: vicinity of El General, alt. 975 m., *Skutch 2914* (GH, Mo); heights of La Carpintera, vicinity of Tres Ríos, *Allen 524* (GH, Mo); Hacienda San Francisco de Guadeloupe, alt. 1150 m., *Pittier 8472* (BR, GH, Mo), *7160* (BR); San José, *Pittier 42* (BR); Piedra Blanca, *Tonduz 1267* (BR). DATA INCOMPLETE: *Tonduz 10025* (BR, GH, K, NY); *Endress 33* (K).

PANAMA: CANAL ZONE: vicinity of Miraflores, *P. & G. White 52* (GH, Mo); Gamboa, *Standley 28511* (GH). CHIRIQUÍ: vicinity of Bajo Mona and Quebrada Chiquero, alt. 1500 m., *Woodson & Schery 592* (Mo); Boquete, alt. 4000 ft., *Davidson 861* (Mo). PANAMÁ: Agricultural Experimental Station at Matías Hernández, *Pittier 6025* (GH, Mo); along the Corozal road, near Panamá, *Standley 26780* (GH); San José Island, about 55 miles s. se. of Balboa, *Johnston 1112* (GH). DATA INCOMPLETE: *S. Hayes 155* (GH), *325* (NY).

CUBA: LAS VILLAS: in Magdalena, Cayamas, *Baker 2400* (UC). ORIENTE: vicinity of Baracoa, *Pollard, Palmer & Palmer 32* (Mo); exact locality lacking, *Ekman 81* (S). PINAR DEL RIO: Sierra de Anafe, *Wilson & Leon 11298* (Mo). ISLE OF PINES: near Nueva Gerona, *Curtiss 234* (Mo).

VIRGIN ISLANDS: SAINT CROIX: Bassin yard, *Ricksecker 80* (Mo), *136* (Mo, NY).

SAINT VINCENT: Chateau Belair, *Beard 1390* (Mo); *H. H. & G. W. Smith 1057* (GH), *1943* (GH).

TOBAGO: Friendship, *R. O. Williams 11041* (TRIN).

TRINIDAD: Laventille Hills near Port-of-Spain, *Broadway 7617* (G, Mo); Chancellor Road, St. Ann, *Broadway 5242* (Mo), *R. O. Williams 11726, 11932* (TRIN); St. Ann, *Broadway 4415A, 4415B* (TRIN); Hort. Trin., Back Lookout, *Broadway 3681* (TRIN).

COLOMBIA: ANTIOQUÍA: Hatillo, *Bro. Daniel 412* (US); Tablaza, Caldas, *Gartner N. 8* (US); vicinity of Medellín, *Robledo & Yepes 24* (US); Medellín, alt. 1500 m., *Archer 730* (US). ATLÁNTICO: Barranquilla and vicinity, *Bro. Elias 609, 1353* (US); Piojó, Los Mameyales, alt. 350–400 m., *Dugand & Garcia B. 2408* (US); Los Pendales, camino a Santacruz, alt. 5–10 m., *Dugand & Jaramillo 2832* (US). BOGOTA: prope S. Fé de Bogota, alt. 1360 hex., *Bonpland s. n.* (P, FM photo, Mo); Gachata, alt. 1600 m., *Triana s. n.* (P). BOLIVAR: Carthagena, *Billberg 496* (S). BOYACA: region of Mt. Chapon, extreme western part of Dept. Boyaca, *Lawrance 157* (US). CALDAS: Chinchiná, alt. 1350–1400 m., *Cuatrecasas 23100* (FM). CAUCA: Popayán, alt. 1700–2000 m., *Lehmann 5522* (US), alt. 1740 m., *Lehmann 3553* (G, US); entre Popayán y Cajeti (Hacia Tambo), alt. 1700 m., *Cuatrecasas 13839* (FM). CUNDINAMARCA: La Vega, alt. 1300 m., *Arbelaez & Cuatrecasas 5344* (US); Sasaima, *Bro. José 25E* (US). MAGDALENA: vicinity of Cristobal Colon, *Broadway 294* (US). NORTE DE SANTANDER: region del Sarare, Hoya del Río Chitagá, sobre La Cubaya, alt. 1600–1800 m., *Cuatrecasas, Schultes & Smith 12143* (US); Ocaña, alt. 3500 pp., *Schlim 210* (BR). SANTANDER: northern slope of Mesa de Los Santos, alt. 1000–1500 m., *Killip & Smith 15388* (US). TOLIMA:

La Virginia Libano, alt. 1200–1500 m., *Pennell 3282* (US). VALLE: norte de Albán, alt. 2100 m., *Dugand & Jaramillo 3058* (US); La Cumbre, Cordillera Occidental, alt. 1500–1700 m., *Pennell 5213* (US); Cordillera Occidental, Vertiente Occidental, alt. 1770–2260 m., *Cuatrecasas 18544, 18623* (FM), *22172* (FM); Alto del Dinde, entre Cartago y Alcala, alt. 1200–1600 m., *Cuatrecasas 22919* (FM). DATA INCOMPLETE: *Cuatrecasas 4682, 7794* (US); *Bro. Heriberto 479* (US).

VENEZUELA: ARAGUA: Maracay, *Cornelio 64* (US), *Vogl 31* (S). CARABOBO: vicinity of Valencia, alt. 400–800 m., *Pittier 8675, 8677* (US). DISTRITO FEDERAL: Las Adjuntas, *Allart 506* (G, NY, US); lower Catuche, wood above Caracas, *Pittier 7535* (US); Caracas and vicinity, *Bailey & Bailey 286* (US). MERIDA: 3 miles west and 2 miles south of Mérida, *Reed 308* (US); Tabay, alt. 1800–1900 m., *Gehriger 447* (G, US); prope coloniam Tovar, *Fendler 123* (Mo.) MIRANDA: between Las Canales and El Encanto, *Lasser 671* (US). ZAMORA: La Union, Edo. Bolivar, *L. Williams 11226* (US).

BRAZIL: BAHIA: Carpicha, *Blanchet 799* (G); Jacobina, *Blanchet 3749* (BR, G, Mo). CEARA: exact locality lacking, *St. Hilaire Al. 156* (P); *Allemao s. n.* (R); *Rocha 6* (US). PARANÁ: vicinity of Paraná, *Dusén, 22* (S). PERNAMBUCO: Tapera, *Pickel 2727, 2727a* (US). RIO DE JANIERO: Serra do Itatiaya, Nopasto, *Sampaio 4143* (R). RIO GRANDE DO SUL: Porto Alegre, *Reineck & Czermak 329* (P). SÃO PAULO: vicinity of São Paulo, *Puiggari 3328* (P), *Vidal s. n.* (R). DATA INCOMPLETE: *Regnell I 102b* (S); Nazareth, *Jobert 1117* (P).

ECUADOR: GUAYAS: vicinity of Guayaquil, *Mille 8* (NY), *198* (US), *Rose & Rose 22453* (NY, US); vicinity of La Chonta, *Rose, Pachano & Rose 23474* (NY, US); 8 km. north of Guayaquil, *Beetle 8941, 8988* (US); Milagro, alt. 50 m., *Hitchcock 20220* (US); vicinity of Las Juntas, *Rose, Pachano & Rose 23302* (US); vicinity of Huigra, *Rose & Rose 22572* (US).

PERU: CAJAMARCA: San Miguel, Urubamba Valley, alt. 1800 m., *Cook & Gilbert 891* (US). CUZCO: Prov. Urubamba, Machupicchu, alt. 2100 m., *Vargas 795* (Mo, US).

BOLIVIA: TARIJA: Carapari, *Fries 1349* (S).

PARAGUAY: Villa Rica, dans les forets, *Balansa 2325* (G, P); Caaguazú, *Balansa 2326* (BR, G, P); Centralis, near Lake Ypacari, *Hassler 11703* (Mo, US).

ARGENTINA: JUJUY: exact locality lacking, *Fries 52* (S). MISIONES: San Ignacio, *Quiroga 7674, 7675* (S).

31. TRIUMFETTA OBSCURA St. Hil. Fl. Bras. Merid. 1:222. 1825. (T.: *St. Hilaire C282* in Herb. Paris.).

Slender shrubs 1–2 m. high; older branches terete, glabrous, the bark with many shallow, longitudinal ridges, minutely lenticellate, the younger stems and inflorescence axes scurfy, slender with few short, coarse, stellate hairs. Leaves elliptical, more than twice as long as broad, sometimes very obscurely 3-lobed, 11–13 cm. long and 4–6 cm. wide, the base cuneate to rounded, never cordate, the tip gradually and narrowly long-acuminate, the serrations double and rather regular, both surfaces very lightly pubescent with few short, stellate hairs, glabrescent; petioles 3–5 cm. long, slender, scurfy, with many short separate tufts of stellate hairs. Inflorescences axillary, rarely terminal, the cymes of 2–3 cymules, the subtending bracts of the same general shape as the vegetative leaves, the flowering peduncles about 3 mm. long, the pedicels 2–3 mm. long, the bracteoles prominent. Flowers hermaphrodite, the buds narrowly oblongoid, 6–8 mm. long slightly before anthesis, the apical appendages about 1 mm. long, lightly stellate-pubescent; sepals elliptical, 6–9 mm. long, greenish with many short separate tufts of stellate hairs without, brownish and glabrate within; petals linear to narrowly obovate, subequalling the sepals, the claw 1–2 mm. long, lightly plumose; gonophore slender,

about 0.5 mm. long, the glands spherical to slightly oblong, about half the length of the gonophore; urceolus short, about 0.25 mm. high, distinctly 5-lobed, lightly ciliate; stamens 20, the filaments retrorsely 4- to 6-serrate; ovary ovoid, about 1 mm. long, the spinules numerous, recurved, the style 5–6 mm. long, the stigma acute. Fruit orbicular, the body 3–4 mm. in diameter at maturity, very lightly pubescent, 3-loculate, each 2-seeded, the spines slender, 100 or more, about 3 mm. long, slightly retrorsely pilosulose; seeds pyriform, small, about 1.5 mm. long and wide, the funicular groove prominent.

Small trailing shrubs usually growing in forests at altitudes of 1000–1500 m., with scattered distribution; flowering and fruiting in its northern range from October to December and in its southern range from January to about the middle of April.

VENEZUELA: MIRANDA: San Antonia, near Las Mostazas, alt. 1200 m., *Allart 266* (NY, US). MONAGAS: between La Sabana de Las Piedras and Cerro Negro, northwest of Caripe, alt. 1200–1500 m., *Steyermark 61822* (FM, Mo).

BRAZIL: DISTRITO FEDERAL: trail between Sylvestre and Paineira, *L. B. Smith 2253* (US). MINAS GERAIS: Fazenda da Cachoeira, Municipio de Tambos, *Barreto 1620* (R). PARANA: Ponta Grossa, in silva, *Dusén 7551* (Mo, S). RIO DE JANEIRO: circa Sabastianopol, *St. Hilaire C2. 82* (P); Sebastianopol, *Martius 87* (BR), *88* (BR, Mo, NY, S); exact locality lacking, *Luschnath s. n.* (S); *Vauthier 431* (G); *Widgren 92* (S). RIO GRANDE DO SUL: Porto Alegre, *Reineck 220* (S). SÃO PAULO: opposite Santos, *Lindberg 692* (BR); Santos, *Mosén 3264* (S); Santa Anna, *Brade 5900* (S). DATA INCOMPLETE: *Ackermann s. n.* (BR); *Burchell 2486* (BR); *Fryer s. n.* (S); *Riedel 109* (BR, S); *Luschnath s. n.* (BR); *Raben 451* (BR).

ARGENTINA: MISIONES: Loreta, in silva, *Ekman 200* (S).

This species may be distinguished from *T. semitriloba* by its narrowly elliptic, nearly glabrate leaves and by the small apical appendages on the sepals. On a fuller knowledge, it is quite possible that *T. obscura* might be assigned a subordinate rank under *T. semitriloba*.

32. TRIUMFETTA ACRACANTHA Hochr. in Ann. Conserv. Jard. Bot. Genève 18:111. 1914. (T.: *Langlassé 505*).

Small shrubs about 1.5 m. tall; branches and inflorescence axes smooth, brownish, glabrescent. Leaves ovate-elliptic, slightly 3-lobed, about 10–11 cm. long and 4–5 cm. wide, the base rounded or obtuse, the tip gradually and narrowly acuminate, rather equally and doubly serrate, both surfaces with very few small tufts of stellate hairs, nearly glabrate; petioles slender, about 4–6 cm. long, slightly pubescent. Inflorescences usually axillary, sometimes terminal, the cymes of 2 cymules rather lax, the bracts elliptical to narrowly ovate, the flowering peduncles 2–3 mm. long, the pedicels about 2 mm. long. Flowers hermaphrodite, the buds oblongoid, 7–8 mm. long slightly before anthesis, slightly constricted towards the base, the apical appendages slender, 2–3 mm. long, glabrescent; sepals oblong, about 8–9 mm. long including the apical appendages, lightly stellate-pubescent without and glabrescent within; petals lanceolate, 3–5 mm. long, the claw about 2 mm. long, sparsely plumose; gonophore stout, about 1 mm. long and 1.5 mm. thick, the glands spherical, about 0.75 mm. long; urceolus about 0.5 mm. high,

indistinctly lobed, lightly ciliate; stamens 20, the filaments smooth, slightly pubescent towards the base; ovary ovoid, about 1 mm. long, the spinules numerous, recurved, the style slender, about 6 mm. long, the stigma briefly 3-lobed. Fruit orbicular, the body about 3 mm. thick at maturity, lightly stellate-pubescent, 3-loculate, each cell 2-seeded, the spines slender, about 75, retrorsely pilosulose.

Small shrub of western Mexico growing at low elevations, usually between altitudes of 100 and 200 m.; flowering and fruiting from September to December.

MEXICO: COLIMA: Manzanillo, *E. Palmer 902* (NY). GUERRERO: Baqueta, alt. 200 m., *Langlassé 505* (G, GH, US); Atoyac, Galeana, alt. 160 m., *Hinton 10911* (GH). SINALOA: La Noria, foothills, alt. 800 ft., *Mexia 333* (UC); Capule, alt. 200 m., *Ortega 6083* (US); Ymala, vicinity of Culican, *E. Palmer 1683* (US); vicinity of Culican, *Brandegee s. n.* (UC).

The glabrescent leaves and sepals, together with the regularity and the fineness of the serrations, clearly distinguish this species from *T. semitriloba.*

33. TRIUMFETTA ALTHAEOIDES Lam. Encyc. Meth. 3:420. 1789. (T.: "Cayenne", *Stoupy s. n.* in Herb. Paris.).

Triumfetta microphylla Vahl, Eclog. Amer. 2:34. 1796. (T.: "Br. Guyana", *von Rohr s. n.* in Herb. Copenhagen).
Triumfetta surinamensis Steud. Flora 26:755. 1843. (T.: *Hostmann 605*).
Triumfetta dichotoma Turcz. in Bull. Soc. Nat. Moscou 32^1:261. 1859. (T.: *Regel 12453*).
Triumfetta semitriloba var. *surinamensis* (Steud.) Hochr. in Ann. Conserv. Jard. Bot. Genève 18:95. 1914.
Triumfetta semitriloba f. *althaeoides* (Lam.) Uittien in Pulle, Fl. Surinam 3:56. 1932.

Bushy, spreading shrubs about 2 m. high; older branches lightly ferruginous-pubescent, the younger ones and the inflorescence axes more densely so, slightly scurfy. Leaves broadly ovate, 12–14 cm. long and 11–13 cm. wide, generally not lobed, sometimes obscurely 3-lobed, the base shallowly cordate, the tip gradually and narrowly acuminate, the serrations rather regular, generally glandular at the base, with 4 prominent glands on the petiole at the basal sinus, the upper surface lightly stellate-tomentose, the lower more densely and coarsely so; petioles 4–6 cm. long, stout, densely tomentose. Inflorescences on terminal branches, the cymes of 3–4 cymules, usually in the axils of the bracts, condensed in dense nodose clusters, the flowering peduncles 3–5 mm. long, the pedicels short, usually 1–2 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, about 6 mm. long at anthesis, the apical appendages about 1 mm. long, nearly obsolete; sepals broadly elliptical, 6–7 mm. long, densely ferruginous-tomentose without, glabrescent within; petals linear, 3–4 mm. long, the claw about 1–2 mm. long, lightly plumose; gonophore stout, about 0.75 mm. long and 1.0–1.5 mm. wide, the glands spherical, small; urceolus short, less than 0.5 mm. high, 5-lobed, lightly ciliate; stamens 20, the filaments glabrous, retrorsely 6-serrate; ovary orbicular, about 1.0 mm. long, the spinules numerous, recurved, the style about 5–6 mm. long, the stigma acute. Fruit orbicular, large, the body 6–8 mm. in diameter at maturity, lightly stellate-pubescent, 4- to 5-loculate, each cell 2-seeded, later falsely 8-loculate with one

Fig. 10. *Triumfetta althaeoides*

seed each, but not more than 6 seeds maturing per fruit, the spines numerous, about 200, slender, about 3 mm. long, retrorsely pilosulose; seeds pyriform, about 2 mm. long and 2.5 mm. wide, the funicular groove rather prominent.

Trinidad and northern South America; commonly growing on loose sandy soil in moist areas, usually at very low elevations, rarely ever being found above an altitude of 200 m.; fruiting and flowering in its northern range from August to November, and in its southern range from April to July.

TRINIDAD: Maraval, *Broadway 7065* (FM, G, Mo, S); Erin, *Broadway 7797* (Mo, S); Inois, *Broadway 8472* (Mo, TRIN); *Collins 4411* (Mo, TRIN); *Alexander 4597* (TRIN); collector not mentioned, *651, 1106* (TRIN).

COLOMBIA: ANTIOQUIA: La Serrania entre ríos Ariari y Meta, en Angostura, alt. 240 m., *Cuatrecasas 7782* (US).

BRITISH GUIANA: vicinity of Bartica, on the Essequibo River, *De la Cruz 1913* (Mo, NY, US); vicinity of Wismar, on the Demerara River, *De la Cruz 2456* (Mo, NY, US);

Waramuri Mission, Moruka River, Pomeroon Dist., *De la Cruz 1009* (US), *2563* (Mo, NY, US); Waini River, Northwest Dist., *De la Cruz 3628* (Mo, NY, UC, US); Wanama River, Northwest Dist., *De la Cruz 3951* (Mo, US); Moruka River, Pomeroon Dist., *De la Cruz 4537* (Mo, US); Penal Settlement, *Hitchcock 17088* (US). DATA INCOMPLETE: *Schomburgk 81* (P); *von Rohr s. n.* (C, FM photo).

SURINAM: prope Poclebantze, *Kegel 57* (P); *Hostmann 605* (Mo, P, U); *Focke 634* (U).

FRENCH GUIANA: Cayenne, *Sagot s. n.* (P), *Soubirou s. n.* (P), *Jelski s. n.* (S, U); vicinity of Cayenne, *Broadway 238, 286* (US). DATA INCOMPLETE: *Le Prieur 117* (P); *C. Richard s. n.* (P); *Leblond s. n.* (P).

BRAZIL: AMAZONAS: Basin of Río Solimoes, Munic. São Paulo de Olivença, near Palmeres, *Krukoff 8460* (BR, Mo, NY). BAHIA: Ilhoes, *Curran 435* (NY, US); *Salzmann 75* (G, Mo). MARANHÃO: Island of São Luiz, *Fröes 11838* (US). MATO GROSSO: Cuiabá, *Malme 1538* (R, S, US); Santa Ana da Chapada, *Malme s. n.* (S). PARÃ: northeast of San Izabel, vicinity of Belem, *F. Drouet 2042* (Mo, R, US); Ilha do Mosqueiro, near Pará, *Killip & Smith 30499* (US); Belem, *Dahlgren & Sella 350, 761* (US), *A. Silva 9* (US), *Baldwin 4524* (US); locality not mentioned, *Goeldi 1097* (NY, US); *Prentiss s. n.* (NY). PERNAMBUCO: Tapera, Recife, *Pickel 3446* (US). RIO DE JANEIRO: Raiz da Serra de Petropolis, *Gomes 68* (R). SÃO PAULO: locality not mentioned, *Burchell 4484, 7218* (BR).

PERU: LORETO: Ost-Peru, Stromgebiet des Maranon von Iquitos, *Tessmann 3592* (S); Balsapuerto, alt. 220 m., *Klug 3054* (Mo, US); Mishuyacu, near Iquitos, alt. 100 m., *Klug 1086, 1289* (US), *Killip & Smith 27240* (US); Punchana, near Iquitos, *L. Williams 1316, 1324* (US); Caballo-Cocha on the Amazon, *L. Williams 2063* (US).

BOLIVIA: COCHABAMBA: exact locality lacking, *D'Orbigny 596* (P). LA PAZ: Mapiri, *R. S. Williams 787* (US).

Despite the fact that this species has often been treated as synonymous with *T. semitriloba,* it is definitely not conspecific with it. Its large orbicular 8-loculate fruit with numerous long slender spines, and its broadly ovate, undivided leaves with 4 conspicuous glands on the petiole at the basal sinus are two of the more important characters which aid in distinguishing this weedy species from *T. semitriloba.*

34. TRIUMFETTA SEMITRILOBA Jacq. Select. Stirp. Amer. Hist. 147. 1763. (T.: *Banks Herb. s. n.* in Herb. Riksmuseet, Stockholm).

Triumfetta triloba Lam. Ency. Meth. 3:420. 1789. (T.: *Commerson s. n.* in Herb. Paris.).
Triumfetta hirta Vahl, Symb. Bot. Pl. 3:63. 1794. (T.: "St. Martha", *Ryan s. n.* in Herb. Copenhagen).
Triumfetta rubricaulis HBK. Nov. Gen. & Sp. 5:342. 1821. (T.: "Caracas", *Bonpland s. n.* in Herb. Paris.).
Triumfetta havanensis HBK. loc. cit. 345. 1821. (T.: "Insula Cuba, prope Havanam", *Bonpland s. n.* in Herb. Paris.).
Triumfetta ovata DC. Prod. 1:507. 1824. (T.: "Antilles", collector unknown in Herb. Deless.).
Triumfetta oxyphylla DC. loc. cit. 508. 1824. (T.: "Novae-Hispaniae", *Sessé & Mociño s. n.* in Herb. Deless.).
Triumfetta tricuspis St. Hil. Fl. Bras. Merid. 1:224. 1825. (T.: "Villa-Rica", *St. Hilaire s. n.* in Herb. Paris.).
Triumfetta acutiloba DC. Pl. Rar. Jard. Genève, 64. 1829. (T.: "Havanne", S. *Burat s. n.* in Herb. Deless.).
Triumfetta Thonningiana DC. loc. cit. 1829. (T.: *Thonning s. n.* in Herb. Deless.).
Triumfetta tiliaefolia Vahl ex DC. loc. cit. 1829. (T.: *West s. n.* in Herb. Deless.).

Fig. 11. *Triumfetta semitriloba*

Triumfetta semitriloba var. *brasiliensis* K. Schum. in Mart. Fl. Bras. 12^3:135. 1886. (T.: *Blanchet 799*).
Triumfetta semitriloba var. *Martiana* K. Schum. loc. cit. 135. 1886, in part. (T.: *Martius 1263*).
Triumfetta semitriloba var. *typica* K. Schum. loc. cit. 1886.
Triumfetta semitriloba havanensis (HBK.) Millsp. in Field Mus. Publ. Bot. 1:507. 1902.
Triumfetta semitriloba var. *Berlandieri* Hochr. in Ann. Conserv. Jard. Bot. Genève 18:95. 1914. (T.: *Berlandier 71*).
Triumfetta Sloanei Fawc. & Rend. in Jour. Bot. 59: 225. 1921. (T.: *Ridley s. n.* in Herb. Kew.).
Heliocarpus hirtus (Vahl) Will. & Sandw. in Fl. Trin. & Tobago 1:111. 1929.

Shrubs 1–2 m. high; older branches terete, glabrescent, the bark reddish, prominently lenticellate, the younger ones and inflorescence axes rough, slender, scurfy,

with short, coarse, stellate tomentum. Leaves generally broadly ovate to 3-lobate, the shape and size extremely variable even on the same plant, usually about 6–8 cm. long and 4–6 cm. wide, the base either cuneate or rounded, very rarely subcordate, the terminal lobe long-acuminate, the laterals usually blunt, but sometimes all 3 lobes narrowly and gradually acuminate, the serrations extremely irregular, usually glandular, both surfaces rather densely and coarsely stellate-pubescent; petioles 3–6 cm. long, slender, scurfy with short, separate tufts of stellate hairs. Inflorescences axillary, rarely terminal, the cymes of 2–3 cymules in the axils of the bracts, the bracts narrowly elliptical, very rarely obscurely 3-lobed, the flowering peduncles 2–3 mm. long, the pedicels about 3 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, about 5–8 mm. long slightly before anthesis, the apical appendages 1–2 mm. long, lightly stellate-pubescent; sepals elliptical, 6–10 mm. long including the apical appendages, greenish and rather lightly stellate-pubescent without, yellow-brown and glabrescent within; petals elliptical to narrowly obovate, subequalling the sepals, the claw 2–3 mm. long, rather densely plumose; gonophore about 0.75 mm. long, rather slender, the glands oblong, about half as long as or subequalling the gonophore; urceolus rather short, 0.25–0.50 mm. high, densely ciliate; stamens 15–25, the filaments glabrous, retrorsely 4-serrate; ovary ovoid, about 1 mm. long, the spinules numerous, recurved, the style 6–8 mm. long, the stigma usually acute, very rarely 3-parted. Fruit orbicular, the body 3–5 mm. in diameter at maturity, lightly to rather densely stellate-pubescent, 3-loculate, each cell 2-seeded, though very rarely all the 6 seeds maturing, the spines 50–75, 2–3 mm. long, slender, retrorsely pilosulose at the base from half to three-quarters of its length; seeds pyriform, about 2 mm. long and wide, the funicular groove prominent.

A common weed of the tropics, which finds its habitat usually in abandoned fields or cut-over forest areas, and in general being a nuisance to both man and his animals, growing from sea-level to about an elevation of 2000 m. It is found principally in the warmer regions of the New World, and less abundantly in tropical Africa. Flowers and fruits in its northern range from October to March, in its central range from December to May, and in its southern range from March to July.

This species may be recognized by its leaves which generally tend to be bluntly 3-lobed, bearing only short, scabrous, stellate hairs on both surfaces, together with either its elongoid flowers, which are 6–10 mm. long with linear-elliptic petals, or its fruits with 3, 2-seeded locules, and about 50–75 retrorsely pilosulose spines.

MEXICO: CAMPECHE: Tuxpeña, *Lundell 953* (Mo). CHIHUAHUA: west of Chuchuichupa, *LeSueur 957* (Mo); Guasaremos, Río Mayo, tropical upper Sonoran margin, *Gentry 1884* (Mo); Hacienda San Miguel, near Batolopes, *E. Palmer 23* (GH, K, US). GUERRERO: Acapulco and vicinity, *E. Palmer 605* (K, Mo, NY, UC). JALISCO: shaded slopes of the barranca near Guadalajara, *Pringle 1756* (BR, K, Mo, MICH); exact locality lacking, *Galeotti 4150* (BR). MORELOS: hills near Yantepec, alt. 4000 ft., *Pringle 9695* (K, Mo). NAYARIT: vicinity of Acaponeta, Tepic, *Rose, Standley & Russell 14212, 14279* (NY); Santiago, Tepic, *Lamb 549* (Mo); Rincon de Mateo, near Yxtlan, alt. 1100 m., *Mexia 775* (Mo); Tepic, *M. E. Jones s. n.* (UC). SAN LUIS POTOSI: en route from San Luis Potosi to Tampico, *E.*

Palmer 1060 (K, Mo); Tamasunchale, *Kenoyer s. n.* (Mo). SINALOA: Las Mesas, Sierra Suratato, alt. 3000 ft., *Gentry 6623* (Mo). SONORA: Sierra de Alamos, rocky canyon slope, alt. 3000 ft., *Gentry 4867* (Mo); Alamos, *E. Palmer 642* (US). TAMAULIPAS: vicinity of Tampico, *E. Palmer 72* (GH); vicinity of Gómez Farias, alt. 350 m., *E. Palmer 270* (Mo); 10 km. northwest of El Progresso, vicinity of Ocampo, alt. 1450 m., *Stanford, Retherford & Northcraft 1048* (Mo). VERA CRUZ: Cordillera, *Galeotti 7040* (P); exact locality lacking, *Müller 204* (NY), *Gounin s. n.* (P). YUCATAN: exact locality lacking, *Gaumer 24450* (Mo).

GUATEMALA: ALTA VERAPAZ: Cubilquitz, alt. 350 m., *Tuerckheim II 227* (BR, S); Cobán, alt. 4000 ft., *H. Johnson 38* (US). PETEN: La Libertas and vicinity, *Aguilar 188* (Mo).

EL SALVADOR: SAN SALVADOR: vicinity of San Salvador, alt. 650–850 m., *Standley 22685* (NY).

COSTA RICA: data incomplete, *Solis R. 6* (Mo).

BERMUDA: Walsingham, *Harshberger s. n.* (Mo), *Flynn 76* (Mo).

BAHAMA ISLANDS: New Providence: Nassau, *Hitchcock s. n.* (Mo); *Curtiss 11* (Mo).

CUBA: HAVANA: prope Havana, *Bonpland s. n.* (P, Mo photo); Santiago de las Vegas, *Hermann 307* (Mo); La Havanne, *de la Otta s. n.* (Mo photo). LAS VILLAS: Santa Clara, Cieneguita, Dist. Cienfuegos, *Combs 115* (Mo). ORIENTE: *Wright 43* (BR, G, Mo, S); Bayate secus vias, *Ekman 2085* (S), *3413* (S); Sierra de Nipe, El Taller ad Rio Piloto, *Ekman 3337* (S).

GRAND CAYMAN: *Hitchcock s. n.* (Mo).

JAMAICA: Port Morant, *Hitchcock s. n.* (Mo); Lucca, *Hitchcock s. n.* (Mo); Farm Hill, *Orcutt 3436* (Mo); mountains near Kingston, *Hansen s. n.* (Mo); *Cumming s. n.* (G); Porto Antonio, *Hitchcock s. n.* (Mo); Lloyd, *Hitchcock 1014* (Mo); Constant Spring, *Ridley s. n.* (K).

HAITI: La Tortue, between Palmiste and Embrouchure de la Thochelle, *Ekman 4184* (S); La Tortue, main ridges at Binquette, *Ekman 4229* (S); Roseaux, valley of Roseaux River, *Seibert 1774* (Mo); prope Sarrasin, *Buch 586* (S).

DOMINICAN REPUBLIC: Dist. Moncion, Prov. Monty Cristy, alt. 375 m., *Valeur 411* (Mo); "Sylvania", alt. 1500–1800 ft., *Cooper III 25* (Mo, NY); St. Domingo City, at Guibia, *Ekman 10945* (S); St. Cristobal, *Tuerckheim 2623* (BR, Mo, S).

PUERTO RICO: Ciales, Bayamon, *Otero 363* (Mo); Rincon, ad Tuntas, *Sintenis 5652* (Mo); near Mayaguez, *Theisohn 30* (Mo), *Blauner 171* (G), *Heller 4444* (Mo).

VIRGIN ISLANDS: SAINT THOMAS: Signal Hill, alt. 1200 ft., *Eggers s. n.* (Mo). SAINT CROIX: Bassin, *Ricksecker 138* (Mo), *225* (FM); *Thompson 1018* (S).

FRENCH WEST INDIES: SAINT BARTHELEMY: *von Goes s. n.* (S); *Forström s. n.* (S). GUADELOUPE: Pointe-à-Pitre, *Hammarlund 29* (S); Cascade Vaugelé, *Picard s. n.* (P); *Beaupertuis s. n.* (P). MARTINIQUE: *Belanger 560, 647* (P); Fort Royal, *Plée s. n.* (P).

SAINT VINCENT: near Kingstown, *Eggers 6940* (S).

BARBADOS: *Wright s. n.* (BR).

TOBAGO: Highmoor, *Broadway 3407* (Mo).

TRINIDAD: *Kuntze 661* (US).

COLOMBIA: MAGDALENA: exact locality lacking, *Bertero s. n.* (Mo).

VENEZUELA: DISTRITO FEDERAL: Los Venados, near Caracas, *Allart 93* (G, NY, US); near Caracas, alt. 450 m., *Bonpland s. n.* (FM photo, Mo). MERIDA: 3 miles west, 2 miles south of Mérida, *Reed 306* (US); near Galipan, on the bank near water, *Pittier 213* (G). MIRANDA: vicinity of Petare, along hills, *Pittier 9894* (G); Hacienda Paloma, alt. 900 m., *Pittier 13052* (GH, Mo, NY, US); in valley on road from El Valle to Cua, along the river, *Pittier 11974* (Mo).

BRAZIL: BAHIA: exact locality lacking, *Blanchet 3117* (G); *Luschnath 163* (BR). DISTRITO FEDERAL: Trapicheiro, *Lutz s. n.* (R). MINAS GERAIS: Campo Tiririca, alt. 590 m., *Mexia 5663* (Mo, R, US); Lagoa Santa, *Da Costa s. n.* (R); Serre Negra, *St. Hilaire 98* (P); Viçosa, Chacha Valley, *Mexia 4733* (Mo, US); exact locality lacking, *Claussen s. n.* (NY), *Martens s. n.* (BR). PARANA: Morretes, Estrada da Graciosa, Grota Funda, *Hatschbach 908* (US). RIO DE JANEIRO: Nova Friburgo, Estrada de Conego,

Velloso s. n. (R); Corcovado, *Saldanha 224, 649* (R); Petropolis, *Sampaio 7692* (R); Campos, *Sampaio 8300* (R); Ipanema, *Diogo 52* (R); Teresopolis, *Emygdio s. n.* (R); Matas do Rio Trapicheiro, *Freire & Peckolt 612, 613* (R). SÃO PAULO: Horto Florestal de Loreto, *Sampaio 4306* (R); Jaraguá, *Brade 5897* (S). DATA INCOMPLETE: *Regnell II 286* (S); *Urteri 12* (G).

ECUADOR: GUAYAS: 21 km. southwest of Guayaquil, alt. 40 m., *Worth, Morrison & Horton 8941* (Mo); Sudl. Naranjapata, alt. 550 m., *Schimpff 587* (Mo, US).

PERU: LIMA: exact locality lacking, *Anderson s. n.* (S). LORETO: lower Río Huallaga, *L. Williams 4360* (US). SAN MARTIN: San Roque, alt. 1350–1500 m., *L. Williams 7160* (US).

BOLIVIA: BENI: Río Chaparé-Mamoré, alt. 250 m., *Werdermann 2166* (Mo); vicinity of Reyes, alt. 1000 ft., *Cardenas 1377* (NY). COCHABAMBA: Prov. Chapare, Wegerand, Socotol, alt. 1500 m., *Steinbach 9089* (S). LA PAZ: Yungas, *Bang 465* (FM, Mo); Mapiri, alt. 2500–5000 ft., *Rusby 1236a* (NY); Prov. Larecaja, near Sorata, alt. 2550 m., *Mandon 826* (BR, NY, S), *827* (G, S); Apolo, *R. S. Williams 103* (NY, US); Polo-Polo bei Coroico, alt. 1100 m., *Buchtien 3840* (S). SANTA CRUZ: Prov. Sara, Buena Vista, Barbechos, Río Surutú, alt. 400 m., *Steinbach 5545* (G, Mo, S); Buena Vista, Orilla-basque, alt. 450 m., *Steinbach 7118, 7416* (Mo, S). DATA INCOMPLETE: *Fries 1506, 1506a* (S).

PARAGUAY: Villarica, *Jörgensen 3858* (Mo, S, US); exact locality lacking, *Morong 132* (NY).

ARGENTINA: JUJUY: en las Cercanias, *Lorentz & Hieronymus 1009* (S); Humahuaca, alt. 2800 m., *Venturi 8369* (S, US); Humahuaca, alt. 3020 m., *Claren 11715* (S). MISIONES: Santa Ana, *Rodriguez 231* (Mo).

35. TRIUMFETTA OLIGACANTHA Hochr. in Ann. Conserv. Jard. Bot. Genève 18:106. 1914. (T.: *Pavon s. n.* in Herb. Deless.).

Small shrubs; branches and inflorescence axes smooth, scurfy, ferruginous-tomentose. Leaves broadly ovate, about 9–10 cm. long and 6–8 cm. wide, the base obtuse, the tip gradually long-acuminate, the serrations rather regular, the basal ones generally glandular, the upper surface lightly stellate-pubescent, the lower more densely so; petioles about 3–6 cm. long, densely pubescent. Inflorescences axillary, the cymes of 3–4 cymules, rather lax, the flowering peduncles about 8–10 mm. long, the pedicels 3–5 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 6–8 mm. long slightly before anthesis, slightly constricted in the middle, the apical appendages large, about 3 mm. long, slightly pubescent; sepals oblong, 8–11 mm. long including the apical appendages, densely tomentose without, glabrescent within; petals narrowly obovate, 6–7 mm. long, the claw 2–3 mm. long, shortly plumose; gonophore slender, about 0.75 mm. long, the glands narrowly elliptical; urceolus small, about 0.5 mm. high, indistinctly lobed, slightly ciliate; stamens about 30, the filaments smooth, glabrous; ovary small, orbicular, about 1 mm. long, the spinules about 35, recurved, the style about 8–9 mm. long, the stigma acute. Fruit orbicular, the body about 2–3 mm. in diameter at maturity, matted cinereous-tomentose, 3-loculate, each cell 1-seeded, the spines 25–40, 2–3 mm. long, retrorsely pilosulose; mature seed pyriform, about 1.5 mm. long and wide, the funicular groove prominent.

Known only from a few collections, mostly from Ecuador, and one (the type) probably from Peru. Apparently rare plants, which are usually found at low elevations. Flowering and fruiting from June to October.

Ecuador: guayas: Duran, Westabhang, alt. 40 m., *Schimpff 1078* (Mo); Guayaquil, alt. 50 m., *Hitchcock 20153* (US). data incomplete: Terecita, *Stevens 161* (US); *Fraser s. n.* (G).

Peru (?): *Pavon s. n.* (G).

Though rather poorly represented in the herbaria, this is one of the more distinct species in the "*semitriloba* complex." It is easily identified by its undivided, caudate-acuminate leaves, by its relatively long apical appendages of the sepals, and also by its fruits, which have only a few (25–40) spines.

36. Triumfetta Lappula L. Sp. Pl. ed. 1. 444. 1753.

Triumfetta heterophylla Lam. Encyc. Meth. 3:420. 1789. (T.: "St. Domingo", *Poiteau s. n.* in Herb. Paris.).
Triumfetta sinuosa Miq. in Linnaea 22:466. 1849. (T.: *Kappler 1589*).
Triumfetta Hostmanni Miq. loc. cit. 1849. (T.: *Hostmann 499*).
Triumfetta Berteri Turcz. in Bull. Soc. Nat. Moscou 31[1]:227. 1858. (T.: *Bertero s. n.* in Herb. Paris.).
Triumfetta Salzmanni Turcz. loc. cit. 229. 1858. (T.: *Salzmann s. n.* in Herb. Paris.).
Triumfetta quinqueloba Turcz. loc. cit. 36[1]:574. 1863. (T.: *Mathews 1625*).

Fig. 12. *Triumfetta Lappula*

Tall weedy shrubs about 1–2 m. high; branches and inflorescence axes with coarse, scurfy, ferruginous tomentum. Leaves broadly ovate, usually pandurate, 3- to 5-lobed, about 8–10 cm. long and 7–9 cm. wide, the base obtuse to rounded, the tips acuminate, the serrations usually glandular, unequal and blunt, the upper surface lightly pubescent, the lower lightly tomentose to more densely so; petioles usually 6–8 cm. long, sometimes slightly longer, usually thick, very densely and coarsely pubescent. Inflorescences axillary, the cymes of 2, rarely 3, cymules, generally condensed, the bracts elliptical, very rarely obscurely 3-lobed, the flowering peduncles about 2–3 mm. long, the pedicels short, 1–2 mm. long. Flowers hermaphrodite, the buds narrowly oblongoid, 3–5 mm. long slightly before anthesis, slightly constricted in the middle, the apical appendages very short, rarely absent; sepals oblong, about 4–6 mm. long, densely stellate-tomentose without, glabrescent and yellowish within; petals absent; gonophore obsolete, the glands absent; urceolus very small, nearly obsolete, not ciliate; stamens usually 10, rarely 15 or 5, the filaments glabrous, smooth; ovary ovoid, about 1.0–1.5 mm. long, the spinules numerous, recurved, the style about 3 times the length of the ovary, the stigma acute, sometimes very briefly 2-fid. Fruit orbicular, the body about 3 mm. in diameter at maturity, lightly stellate-pubescent, 3-, sometimes 2-, loculate by abortion, the spines about 50, slender, 2–3 mm. long, retrorsely pilosulose; seeds pyriform, about 1.5–2.0 mm. long and 1.0–1.5 mm. wide.

A widespread species found abundantly in the tropical Americas and less so in the eastern hemisphere. Usually growing in open places and a nuisance in cultivated paddocks, it finds its habitat from sea-level to an altitude of about 2000 m. Flowers and fruits from late November to early March.

The absence of petals, gonophore, and urceolus in flower, and the retrorsely pilosulose spines, the small body and the absence of glandular gonophore in fruit, are some of the more constant characters which facilitate the identification of this species.

MEXICO: CAMPECHE: Tuxpeña, *Lundell 1188* (Mo). CHIAPAS: Escuintla, *Matuda 97* (Mo). YUCATAN: exact locality lacking, *E. P. Johnson 58* (NY).

BRITISH HONDURAS: Mullins River road, alt. 100 ft., *Schipp 868* (Mo).

HONDURAS: MORAZÁN: Francisco, along Yeguare River, alt. 900 m., *Williams & Molina 12202* (Mo). ATLANTIDA: above San Juan, west of Tela, *Yuncker 4810* (Mo).

EL SALVADOR: SAN SALVADOR: vicinity of San Salvador, alt. 650–850 m., *Standley 19091* (Mo).

NICARAGUA: CHINANDEGA: near Chinandega, *Baker 2247* (K, Mo); Volcán El Viejo, *Baker 17* (Mo). GRANADA: envr. de Granada, alt. 410 m., *Lévy 399* (G, P).

COSTA RICA: GUANACASTE: buissons autour de Nicoya, *Tonduz 13491* (G, NY, P, US). SAN JOSÉ: taillis du Rodeo de Pacaca, alt. 900 m., *Pittier 3258* (BR); au Rodeo, alt. 700–1000 m., *Pittier 1630* (BR); vicinity of El General, alt. 880 m., *Skutch 3028* (Mo). DATA INCOMPLETE: près San Mateo, alt. 200 m., *Biolley 7059* (BR); brussailles du Río Ceibo, alt. 200 m., *Pittier 6693* (BR).

PANAMA: BOCAS DEL TORO: vicinity of Chiriquí Lagoons, Old Bank Island, *Wedel 1883, 1949, 2005* (Mo); Water Valley, *Wedel 1710, 1779, 1825, 1847, 1854* (Mo); Darkland, *Wedel 2618* (Mo); Boca, littoral Atlantique, *Tonduz 9153* (BR). CANAL ZONE: Barro Colorado Island, *Shattuck 728* (Mo); vicinity of Miraflores Lake, *P. White 279* (Mo); Ancón Hill, alt. 600 ft., *R. S. Williams 21* (NY); vicinity of San Carlos, alt.

10 m., *Allen 1138* (Mo); Chagres, Isthmus of Panama, *Fendler 172* (Mo); hills between Capira and Potrero, alt. 80–130 m., *Dodge & Hunter 8626* (Mo). DATA INCOMPLETE: S. *Hayes 321, 370, 991, s. n.* (NY); *Mell s. n.* (NY).

CUBA: SANTA CLARA: Colonia Limones, Ingenio Soledad, near Cienfuegos, *Pringle 93* (Mo). ORIENTE: Santiago de las Vegas, *Baker 84* (Mo, NY, P, U); Cooper's Ranch, base of El Yunque, Mt. Baracoa, *Underwood & Earle 578* (NY). DATA INCOMPLETE: *Serre s. n.* (BR).

ANTIGUA: *Wullen s. n.* (BR).

GRAND CAYMAN: *Hitchcock s. n.* (Mo).

JAMAICA: Gray's Inn, *Orcutt 4664* (Mo); above Kingston, *Lehmann 1292* (NY); Port Morant, *Hitchcock s. n.* (Mo); Constant Springs, *Hitchcock s. n.* (Mo).

DOMINICAN REPUBLIC: Sonador, Bonao, La Vega, alt. 180 m., *Valeur 381* (Mo, NY); prope Barahona, *Fuertes 179* (Mo).

PUERTO RICO: on the Adjuntas road, 7 miles from Ponce, *Heller 6184* (Mo); Bayamon District, Santurce, *Otero 462* (Mo); Signal Hill, alt. 1100 m., *Eggers s. n.* (Mo).

VIRGIN ISLANDS: SAINT THOMAS: *Eggers 58* (S); *Krebs s. n.* (U). SAINT CROIX: Bassin yard, *Ricksecker 135* (Mo); *Benzon s. n.* (Mo).

MARTINIQUE: *Duss 1363* (Mo); *Belanger 31* (P); *Hahn 224* (P).

TOBAGO: Rocky Vale, *Broadway 3383* (Mo, S); near the Yaws Hospital, Scarborough, *Broadway s. n.* (Mo); top of Lambeau, near King's Bay, *Freeman 10254* (Mo, TRIN).

TRINIDAD: road to Blue Bassin, *McLean 7725* (Mo, TRIN); Carenage, *Fitzsimmons 3847* (TRIN); *Collins 4433* (TRIN); Chancellor's Road, *Broadway 10253* (TRIN); Diego Martin, *Reece s. n.* (TRIN); near Williamsville, *Broadway 9362* (G, U); Moruga, *Britton & Broadway 2454* (US); *Salzmann 250* (Mo).

COLOMBIA: ATLÁNTICO: Los Pendales, Hacienda Ríodulce, alt. 20–50 m., *Dugand & Jaramillo 4139* (US); Los Pendales, cerca de la laguna de Sábalo, alt. 10–30 m., *Dugand & Jaramillo 2704* (US). CAUCA: Popayán, *Garcia B. 4493* (US). LOS LLANOS: Int. El Meta, Villavicencio, alt. 500 m., *Cuatrecasas 4528, 4683* (US). MAGDALENA: Poponte, Magdalena Valley, *Allen 702* (Mo); Curinquita, *H. H. Smith 1908a* (NY). NORTE DE SANTANDER: region del Sarare, El Blanco, confluncia de los ríos Cubugón y Cobaria, alt. 320 m., *Cuatrecasas 13153* (US). SANTA MARTA: exact locality lacking, *H. H. Smith 1600* (BR, Mo, US). TOLIMA: Falán, region de Calamonte, alt. 1120 m., *Garcia B. 8380* (US). VALLE: plano del Valle del Cauca, entre Cabuyal y La Solorza, alt. 1000 m., *Cuatrecasas 14439* (FM, US); Río Canaveralejo, alt. 100 m., *Dryander 2232* (US).

VENEZUELA: DISTRITO FEDERAL: Cordillera del Avila, dry south-facing slopes above Caracas, alt. 1065–1520 m., *Steyermark 55179* (FM, Mo); Puerto La Cruz, alt. 10 m., *Pittier 11640* (G, US); La Guaira, *Boldingh s. n.* (U). MÉRIDA: prope coloniam Tovar, *Fendler 1918* (K). MIRANDA: La Malva near Las Mostazas, *Allart 278* (G, NY, US). SUCRE: Paria Peninsula, Cariaquita, *Bond, Gillin & Brown 5* (US). TRUJILLO: La Concepcion, alt. 2500 ft., *Reed 1041* (US); vicinity of Cristobal Colon, Aricagua, *Broadway 174, 405* (US). DATA INCOMPLETE: *Mathews 1625* (K).

BRAZIL: MARANHÃO: Island of São Luiz, *Froes 11839, 11852* (US). PARÃ: Boa Vista, *Carr s. n.* (US); exact locality lacking, *Sieber s. n.* (BR). DATA INCOMPLETE: *Martius A. 1264* (Mo).

ECUADOR: GUAYAS: Milagro, alt. 50 m., *Hitchcock 20221, 20239* (US). JUNIN: La Merced, alt. 700 m., *Killip & Smith 23419* (US).

PERU: LORETO: Balsapuerto, alt. 200 m., *Klug 3093* (Mo, US). SAN MARTIN: Chazuta, Río Huallaga, alt. 260 m., *Klug 4150* (Mo, US); Iquitos, alt. 100 m., *Killip & Smith 27234* (US).

BOLIVIA: COCHABAMBA: vicinity of Guanai, *Bang 1597* (Mo, S, US). LA PAZ: Charopampa, Mapiri, *Buchtien 1825* (US).

37. TRIUMFETTA **sericata** Ko Ko Lay, sp. nov.

Frutex circiter 1.5–2.0 m. altus. Ramuli graciles dense pubescentes pilis ferrugineis et stellatis et simplicibus. Folia late ovata vel profunde 3-lobata 9–12 cm. longa 7–10 cm. lata base rotundata vel subcordata apice longe acuminata

margine irregulariter serrata interdum glandulosa utrinque scabratis pilis dense canescenti-tomentosis; petiolis 7–10 cm. longis dense tomentosis. Inflorescentiae terminales, cymis cymulis 5–6, bracteis ovatis vel obscure 3-lobatis, pedunculis 2–3 mm. longis, pedicellis 2–4 mm. longis. Flores hermaphroditi, alabastro maturo oblongoideo 6–8 mm. longo; sepalis ellipticis circiter 8 mm. longis extra longe et dense stellato-tomentosis, appendiculis circiter 2 mm. longis dense plumosis; petalis ellipticis 6–7 mm. longis, unguilo circiter 2 mm. longo extra breviter plumoso; gonophoro 0.25–0.5 mm. longo, glandulis quadrangularibus circiter 0.1 mm. latis; urceolo 0.25 mm. alto non-lobato breviter ciliato; staminibus 15, filamentis usque ad 5–6 mm. longis glabris; ovario ovoideo 0.5–1.0 mm. longo, spinulis 40–50 recurvatis, stylo glabro 6–7 mm. longo, stigmate acute vel breviter 3-fido. Fructus globosus non dehiscens, corpore ipso 2–3 mm. diametro breviter stellato-pubescens mox glabrescens, 3-locularis, loculis 1-spermis, aculeis circiter 50, 2.0–2.5 mm. longis irregulariter plumosis; seminibus ovoideo-acutis circiter 0.75 mm. longis et latis.

Northwestern South America growing in open places at altitudes of 1000 to 1300 m.; flowering and fruiting from August to early December.

COLOMBIA: CAUCA: La Manuelita, near Palmira, eastern side of Cauca Valley, alt. 1100–1300 m., *Pittier 794* (NY, US); El Bordo, *Garcia B. 4472* (US). CUNDINAMARCA: El Colegio, *Joseph s. n.* (US). TOLIMA: Honda, *Joseph s. n.* (US). VALLE: Municipio de Candelaria, sur de Palmira, alt. 1200 m., *Nuñez, Araque & Barkley 18. VC. 025* (holotype in Herb. Mo. Bot. Gard. and isotype in U. S. Nat. Herb.).

ECUADOR: exact locality lacking, *Jameson s. n.* (US).

The densely tomentose leaves, the small oblongoid floral buds in dense nodose clusters, the 15 stamens and the small, dark, very lightly pubescent fruits distinguish this species. Though it has a striking superficial resemblance to *T. abutiloides*, it is not closely related to it. Its relationship with any known South American species is rather doubtful. However, it is closest to *T. brachistacantha*, known only from Oaxaca, Mexico.

38. TRIUMFETTA BRACHISTACANTHA Standl. in Field Mus. Publ. Bot. 11:167. 1936. (T.: *Bossé 8019*).

Older branches glabrate, longitudinally ridged, with many prominent white lenticels, the younger stems and inflorescence axes terete, lightly stellate-pubescent. Leaves broadly ovate, small, 1.5–2.0 cm. long and about 1.0 cm. wide, obtuse to subcordate at the base, gradually and narrowly acuminate, rather regularly and doubly serrate, the upper surface lightly stellate-pubescent, the lower more densely so; petioles short, usually not longer than 1 cm., lightly stellate-pubescent. Inflorescences axillary, the cymes of 1 or 2 cymules, rather lax, the flowering peduncles about 3 mm. long, the pedicels 3–4 mm. long. Flowers hermaphrodite, the buds broadly oblongoid, 5–7 mm. long slightly before anthesis, the apical appendages short, about 1 mm. long or less; sepals lanceolate, 7–8 mm. long including the apical appendages, lightly stellate-pubescent without; petals broadly obovate, 5–6

mm. long and 2–3 mm. wide, the claw 2–3 mm. long, densely plumose; gonophore very short, less than 0.5 mm. long, the glands oblong, small; urceolus rather short, about 0.25 mm. high, distinctly 5-lobed, briefly ciliate; stamens 15, the filaments glabrous, smooth; ovary orbicular, about 1 mm. long, the spinules numerous, recurved, the style 4–5 mm. long, the stigma acute. Fruits orbicular, small, loosely borne in small nodose clusters, the body 2–3 mm. in diameter at maturity, lightly stellate-pubescent, 3-loculate, each cell 1-seeded, the spines about 75–100, about 1 mm. long, glabrous; seeds ovoid, 1.5–2.0 mm. long and 1.0–1.5 mm. wide.

Known only from the type.

MEXICO: OAXACA: Chivela, *Bossé 8019* (FM).

39. TRIUMFETTA BARTRAMIA L. Syst. ed. 10. 1044. 1759. (Based on *Bartramia indica*).[35]

Bartramia indica L. Sp. Pl. ed. 1. 389. 1753. (T.: specimen from Hermann's Herb. now in Herb. Mus. Brit.).
Triumfetta rhomboidea Jacq. Select. Stirp. Amer. Hist. 147. 1763.
Triumfetta rhombeaefolia Sw. Prod. Veg. Ind. Occ. 76. 1788. (T.: *Swartz s. n.* in Herb. Riksmuseet, Stockholm).
Triumfetta angulata Lam. Encyc. Meth. 3:421. 1789.
Triumfetta eriocarpa St. Hil. Fl. Bras. Merid. 1:224. 1825. (T.: *Gaudichaud s. n.* in Herb. Paris.).
Triumfetta Lappula Vell. Fl. Flum. 5:*t. 5*. 1827, non L.
Triumfetta Martiana Turcz. in Bull. Soc. Nat. Moscou 31[1]:228. 1858. (T.: *Martius 1263*).
Triumfetta semitriloba var. *Martiana* K. Schum. in Mart. Fl. Bras. 12[3]:135. 1886, in part. (T.: *Martius 1263*).
Triumfetta rhomboidea var. *Spruceana* K. Schum. loc. cit. 133. 1886. (T.: *Blanchet 188*).
Triumfetta excisa Urb. Symb. Ant. 5:413. 1908. (T.: *Sintenis 17c*).
Triumfetta rhomboidea var. *recifensis* Monteiro, in Lilloa 3:247. 1938. (T.: *Monteiro 218b*).

Tall perennial shrubs 1–3 m. high; older branches reddish-brown, glabrous, rough, longitudinally ridged, punctate with prominent white lenticels, the younger ones and inflorescence axes terete or with very shallow longitudinal ridges, scurfy, clothed with short dense rough stellate tomentum. Leaves typically broadly ovate to rhombic-ovate, obscurely or distinctly 3-lobed, often rather deeply dissected into 3 to 5 lobes, usually 4–5 cm. long and nearly as broad, sometimes 7–8 cm. long and 6–7 cm. wide, obtuse or rounded at the base, abruptly acuminate, the serrations irregular, blunt, rarely glandular near the basal sinus, both surfaces nearly glabrate with few scattered, short, coarse, stellate hairs; petioles slender, 3–5 cm. long, briefly stellate-tomentose, scurfy. Inflorescences axillary, the cymes of 3–5 cymules, condensed in dense nodose clusters, the bracts narrowly ovate, petioles usually about 1 cm. long, the flowering peduncles 1–2 mm. long, the pedicels about 1 mm. long. Flowers hermaphrodite, the younger buds obovoid with very deeply cucullate sepals, the older ones oblongoid, the apex more expanded than the base or the middle, 5–7 mm. long slightly before anthesis, lightly stellate-

[35] The identity of this species is based on the interpretation of Fawcett & Rendle in Jour. Bot. 59:224. 1921.

pubescent to glabrescent without, brownish and glabrescent within; petals yellow to brown, broadly obovate, about 5 mm. long and 2–3 mm. wide, the claw 1–2 mm. long, densely plumose; gonophore very short, less than 0.5 mm. long, the glands oblong, very small; urceolus short, deeply many-lobed, briefly ciliate; stamens 10–15, the filaments glabrous with 4–6 rows of retrorse serrations; ovary orbicular, about 1 mm. long, the spinules numerous, recurved, the style 5–6 mm. long, the stigma acute. Fruits small, orbicular, in dense nodose clusters, the body about 3–4 mm. in diameter at maturity, densely cinereous-tomentose, 3-loculate, each cell 1-seeded, the spines numerous, 75–100, about 1.0–1.5 mm. long, glabrous or nearly so; seeds ovoid, about 1.5 mm. long and 1.0–1.5 mm. wide.

A common weedy species of lowland tropics of both hemispheres, but apparently very rare on the continent of North America. Found in Florida and British Honduras where introduced. Flowers and fruits from July to November.

The small round fruits with dense cinereous tomentum between the short glabrous spines and the younger floral buds with very deeply cucullate sepals are constant characters throughout its wide range.

U. S. A.: FLORIDA: Sumter Co., Webster, *Curtiss 6738* (Mo).
BRITISH HONDURAS: Stann Creek, *Schipp 833* (Mo).
JAMAICA: *Swartz s. n.* (S).
HAITI: presqu'ile du Nord-ouest, *Ekman H9663* (S).
DOMINICAN REPUBLIC: Moncion, Prov. Monte Cristi, alt. 375 m., *Valeur 411* (NY, S),
PUERTO RICO: prope Mayaguez ad Guanajibo, *Sintenis 17* (C, S), *17c* (S); Coamo, *Sintenis 3134* (S).
VIRGIN ISLANDS: SAINT THOMAS: *Holton s. n.* (NY). SAINT CROIX: *Ricksecker 136b* (FM); Bassin yard, *Ricksecker s. n.* (NY); *Benzon 214* (C).
MARTINIQUE: *Duss 1364* (Mo); *Sieber 130* (Mo).
TOBAGO: Highmoor, *Broadway 3092* (Mo, S, U); near Frenchfield, *Egger 5633* (S); Dist. Les Coteaux, *Broadway 9071* (Mo).
TRINIDAD: Icacos, *R. O. Williams 10840* (TRIN); *Sieber 150* (G, Mo).
COLOMBIA: MAGDALENA: Santa Marta, Minca, *Engstedt 61* (S).
VENEZUELA: BOLIVAR: Ciudad Bolivar, alt. 35 m., *Holt & Gehriger 158* (US).
FRENCH GUIANA: vicinity of Cayenne, *Broadway 559* (US).
BRAZIL: AMAZONAS: Rio Negro, *Ule 8916* (S, US). BAHIA: Corcovado, antigua estrada, *Glaziou 1148* (BR, C, R); Andaarahy, porto de Tijuca, *Glaziou 8274* (R); vicinity Bahia, *Rose & Russell 19638* (NY, US), *Blanchet 188, 410* (G), *1285B* (BR, P), *s. n.* (Mo); exact locality lacking, *Salzmann 76* (G), *Martius 1263* (BR, G, NY), *1265* (BR); *Glocker 1* (US). DISTRITO FEDERAL: Ilha de Taboinha, Guanabara, *Vidal s. n.* (R); exact locality lacking, *Lutz s. n.* (R); *Lima s. n.* (R). GOYAZ: Porto Imperial, *Burchell 8747* (BR). MATO GROSSO: Santa Anna da Chapadas, *Malme 3407* (S). MINAS GERAIS: Jard. Bot. Belo Horizonte, *Barreto 7925* (R); Fazienda da Chicaca, Munic. Santa Luzia, alt. 1100 m., *Assis 69* (US). PARÁ: Boa Vista on the Tapajoz River, *da Costa 151* (US). PERNAMBUCO: Tapéra, *Pickel 3278* (US). RIO DE JANIERO: Lünd ad Rio de Janeiro, *Warming 1270* (C); Engenhoça, *Warming 1241, 1255, 1259* (C); Atafona, *Sampaio 8142, 8991, s. n.* (R); estrada de Rodagem, Mericá, *Vidal s. n.* (R); Campo Bello, Carrapicho, *Sampaio 4624* (R); Vermelha, *da Costa 50114* (R); Campos, *Sampaio 50117* (R); Caxias, *Passarelli s. n.* (R); prope Rio, *Luschnath s. n.* (S); environs de Rio Janeiro, *Wedel s. n.* (BR); montagne des Orgues, alt. 800 m., *Wagner s. n.* (BR); prope Río-Janeiro, *Burchell 2939* (BR, P); exact locality lacking, *Houllet s. n.* (BR); *Meyen s. n.* (BR); *Lehmann s. n.* (BR); *Burchell 1043* (BR); *Glaziou 667, s. n.* (BR); *Anderson s. n.* (S); *Dusén 77* (S); *Valentin s. n.* (S); *Gartner 14* (US). SÃO PAULO: Campinas, *Heiner s. n.* (S); Santos, *Valentin s. n.* (S). DATA INCOMPLETE: *Alfont s. n.* (S);

Blanchet s. n. (G); *Cordoso s. n.* (R); *Gaudichaud s. n.* (P); *Kiedel 108, 110* (C, S); *Poblius s. n.* (BR); *St. Hilaire s. n.* (BR); *Widgren 534* (S).

Peru: loreto: Iquitos, alt. 100 m., *Killip & Smith 27229* (US); Punchana, near Iquitos, *L. Williams 1314* (US).

40. Triumfetta Sampaioi Monteiro, in Lilloa 3:244. 1938. (T.: *da Costa 65A*).

Shrubs 1–2 m. high; branches and inflorescence axes terete, with few long, stellate and simple hairs. Leaves broadly ovate to deeply 3-lobed, about 9 cm. long and 3 cm. wide, the base cuneate to obtuse, the tip gradually and narrowly acuminate, regularly and doubly serrate, both surfaces with few long, stellate and simple hairs, especially on the veins; petioles about 3 cm. long, densely clothed with long hairs. Inflorescences axillary, the cymes of 4 cymules, condensed in the axils of the bracts, the flowering peduncles about 4 mm. long, the pedicels 1–2 mm. long. Flowers hermaphrodite, the buds oblongoid, small, about 3 mm. long slightly before anthesis, apical appendages prominent though short; sepals oblong, deeply cucullate in younger buds, about 3.5 mm. long, pilose without, glabrescent within; petals narrowly obovate, subequalling the sepals, the claw about 1.5 mm. long, very lightly plumose; gonophore about 0.75 mm. long, the glands quadrangular, small; urceolus absent; stamens 5, the filaments with 4 rows of retrorse serrations, pubescent at the base; ovary orbicular, about 1 mm. long, the spinules about 50, recurved, the style 3–4 mm. long, the stigma very briefly 3-parted. Fruit suborbicular, small, in dense nodose clusters, the body about 3 mm. in diameter at maturity, rather densely long-tomentose, 3-loculate, each cell 1-seeded, the spines 30–50, about 1 mm. long, plumose; seeds pyriform, small.

Known only from northeastern Brazil; flowering and fruiting from March to June.

Brazil: ceara: Maracanahù, Est. Exp. de Pl. Texteis em S. Antonio, *Rodriguez 26* (R); Crato in Caapuerao, *Löfgren 619* (S); exact locality lacking, *Rocha 25* (R). maranhão: Island of São Luiz, *Fröes 11884* (US). para: Río Murucutu, Belem, *da Costa 65A* (R); Belem, Carrapicho, *Silva s. n.* (US).

This species is very closely related to *T. Bartramia,* and the superficial resemblance is rather striking. However, the absence of the urceolus, the presence of only 5 stamens, and the plumose spines differentiate it sufficiently.

41. Triumfetta paniculata Hook. & Arn. Bot. Beechey Voy. 279. 1841. (T.: *Beechey Herb. s. n.* in Herb. Kew.).

Heliocarpus tigrinus Hochr. in Ann. Conserv. Jard. Bot. Genève 18:123. 1914. (T.: *Langlassé 708*).
Triumfetta tigrina (Hochr.) Standl. in Contr. U. S. Nat. Herb. 23:1674. 1926.
Triumfetta leiocarpa Standl. in Field Mus. Publ. Bot. 11:167. 1936. (T.: *Emrick 130*).
Triumfetta Matudai Lundell, in Contr. Univ. Mich. Herb. 7:27. 1942. (T.: *Matuda 2148*).

Small trees or shrubs 3–5 m. high; older branches glabrous, generally angled with decurrent petiole bases, the younger stems and inflorescence axes longitudinally ridged, clothed with short separate tufts of stellate hairs. Leaves broadly ovate, profoundly 3- to 5-lobed, about 15–18 cm. long and 16–20

cm. wide, lightly pubescent, usually scabrous, the veins densely tomentose; petioles 4–7 cm. long, coarsely stellate-pubescent. Inflorescences terminal, the cymes of 3–5 cymules, usually in dense nodose clusters, the flowering peduncles 3–5 mm. long, the pedicels 2–5 mm. long. Flowers hermaphrodite, the buds obovoid, 5–7 mm. long and about 3 mm. wide slightly before anthesis, constricted towards the base, the apical appendages short, nearly obsolete; sepals obovate, about 6 mm. long, with short rough stellate hairs without, glabrescent within; petals linear, yellow to brown, 3–4 mm. long, the claw about 1 mm. long, densely plumose; gonophore short, about 0.5 mm. long, the glands spherical to slightly elliptical, small; urceolus short, 0.25–0.50 mm. high, many-lobed, lightly ciliate; stamens 30–40, the filaments glabrous, smooth; ovary orbicular, about 1.5 mm. long, the spinules numerous, recurved, the style 2–3 mm. long, the stigma briefly 2-parted. Fruit globose, large, the body about 6 mm. in diameter at maturity, glabrous, 2-loculate, each cell 2-seeded, later falsely 4-celled, each with 1 seed, the spines numerous, glabrous, 3–5 mm. long; seeds ovoid, 2–3 mm. long and 1.5–2.5 mm. wide.

Western Mexico, usually growing in oak forests at altitudes of about 500 m.; flowering and fruiting from September to early December.

MEXICO: CHIAPAS: Escuintla, *Matuda 2148* (FM, MICH, NY). COLIMA: Coahuayana, *Emrick 130* (FM). GUERRERO: La Morena, alt. 450 m., *Langlassé 708* (G, GH); Vallecitos, Montes de Oca, *Hinton 11602* (GH). JALISCO: exact locality lacking, *Beechey Herb. s. n.* (K). SINALOA: Quebrado de Mansana, Sierra Surotato, alt. 4000–4500 ft., *Gentry 6507* (Mo); in the foothills of Sierra Madre, *Rose 1768* (US); San Ignacio, San Juan, *Ortega 6880* (FM); exact locality lacking, *Ortega 4768* (US).

Hooker and Arnott gave only a brief description of the spines and referred to three rather brief diagnoses by Schlechtendal[36] for the descriptions of the flowers and the habit. Schlechtendal's descriptions were based on plants collected by Schiede and Deppe. None of the descriptions are adequate, and because of this, *T. paniculata* has been little known in the herbarium. The decurrent petiole bases on the stems, the large, usually 3- to 5-lobed glabrous leaves, the small obovoid floral buds, and the relatively large glabrate fruits, characterize this species. The ebracteolate, terminal inflorescence tends to confuse this species with the genus *Heliocarpus*.

42. TRIUMFETTA GALEOTTIANA Turcz. in Bull. Soc. Nat. Moscou 32[1]:260. 1859. (T.: *Galeotti 4153*).

Triumfetta apetala Hochr. in Ann. Conserv. Jard. Bot. Genève 18:97. 1914. (T.: *Galeotti 4152*).

Shrubs 2–3 m. high; branches and inflorescence axes scurfy, coarsely stellate-tomentose. Leaves broadly ovate to 3-lobed, 7–12 cm. long and 4–8 cm. wide, sometimes slightly larger, the base rounded or subcordate, the tip gradually and narrowly acuminate, the serrations irregular, acute, the basal ones generally glandular, both surfaces scabrous, clothed lightly with many short tufts of stellate hairs,

[36] Schlecht. in Linnaea 5:288. 1830; 6:424. 1831; 11:376. 1836.

Fig. 13. *Triumfetta Galeottiana*

the veins densely tomentose; petioles 3–5 cm. long, coarsely stellate-pubescent. Inflorescences gynodioecious, axillary, rarely terminal, hermaphrodite, large and spreading, the cymes of 3–5 cymules, usually in dense nodose clusters, the flowering peduncles 3–5 mm. long, the pedicels 2–4 mm. long, the buds obovoid, 5–7 mm. long and about 3 mm. wide slightly before anthesis, constricted towards the base, the apical appendages short, nearly obsolete, the sepals obovate, about 6 mm. long, with short rough stellate hairs without, glabrescent within, the petals linear, yellow to brown, 3–4 mm. long, the claw about 1.5 mm. long, densely plumose,

the gonophore slender, 1.0–1.5 mm. long and about 0.75 mm. wide, the glands oblong, prominent, the urceolus about 0.5 mm. high, many-lobed, densely ciliate, the stamens 20–30, the filaments retrorsely 2-serrate, the ovary ovoid, about 1 mm. long, the spinules about 50, recurved, the style less than twice the length of the ovary, the stigma very briefly 3-parted; pistillate inflorescence of the same general nature and size as the hermaphroditic one, the buds oblongoid, about 3–4 mm. long slightly before anthesis, the apical appendages nearly obsolete, the sepals 3–5 mm. long, with short separate tufts of stellate hairs without, glabrescent within, the petals absent, the gonophore elongate, about 1.5 mm. long, the glands oblong, prominent, the urceolus about 0.5 mm. high, many-lobed, densely ciliate, the staminodes 15–20, about 2 mm. long, the ovary orbicular, the spinules about 50, the style about twice the length of the ovary, the stigma very briefly 3-parted. Fruit globose or subglobose, the body glabrous, 3–4 mm. in diameter at maturity, 3-loculate, each cell 1-seeded, the spines 30–40, each 3–4 mm. long, straight, glabrous; seeds pyriform, 1.5–2.0 mm. long and about 1.5 mm. wide.

Southern Mexico, in dry sunny places at altitudes of 500 to 2000 m.; flowering in September and October, the fruit maturing from late October to middle of December.

MEXICO: GUERRERO: Mancho, Mina, alt. 1200 m., *Hinton 9641, 9642, 9643, 9644, 9670* (GH); Zihuagio, Mina, alt. 1100 m., *Hinton 9720* (GH); Río Frio, Mina, alt. 1300 m., *Hinton 10717* (Mo, US), *10718* (GH); Pilas, Mina, alt. 1600 m., *Hinton 10744* (US); Carrizo-Sto. Domingo, Galeana, alt. 1200 m., *Hinton 14371, 14638* (GH); between Petatlan and Chilapa, alt. 5000–6500 ft., *Nelson 2155* (US); San Geronimo, *Altamirano 659* (US). JALISCO: near Etzatlan, *Rose & Painter 7520* (NY, US); between Atequiza and Chapala, *Rose & Painter 7609* (US). MÉXICO: Distr. Temascaltépec: Carboneras, alt. 2000 m., *Hinton 1857* (Mo), *5077, 6827* (US); Ixtapan, alt. 1000 m., *Hinton 2278* (US); Nanchititla, *Hinton 5249* (US); Las Mesas, *6415, 6784* (Mo, US); Tejupiko, *Hinton 6777* (Mo). MICHOACAN: vicinity of Morelia: Coronilla, alt. 1900 m., *Arsène 2540* (Mo, US); Loma Sta. Maria, alt. 1950 m., *Arsène 2978* (GH, Mo, US), *5879* (GH, Mo, NY, US), *7281* (US); Coalcomán, Salitro-Mesa, alt. 1800 m., *Hinton 12484, 12485* (US); Zitacuaro, alt. 1400 m., *Hinton 13340* (GH, Mo); south of Torricillas, *Hinton 15281* (GH, US); Tancitaro, Uruapan, *Hinton 15681* (GH). NAYARIT: road from Tepic to Los Aguacates, alt. 1000 m., *Mexia 583a* (US); trail from Tepic to Santiago, alt. 1000 m., *Mexia 639* (Mo, US). OAXACA: Cerro de San Felipe, 1900 m., *Conzatti 453* (US), *1617* (NY, US); Valley of Etla, *Alvarez 728* (GH, US); Zinatlan, alt. 1925 m., *Conzatti & Velde 4676* (BR); exact locality lacking, *Moricand s. n.* (G). SINALOA: Las Mesas, Sierra Surotato, alt. 3000 ft., *Gentry 6142* (Mo); Quebrado de Mansana, Sierra Surotato, alt. 4000–5000 ft., *Gentry 6454, 6454a, 6454b, 6454c, 6561* (Mo). VERA CRUZ: Zacuapan, Cordillera, alt. 3000 ft., *Galeotti 4152* (BR), *4153* (BR, G, US); Orizaba, *Botteri s. n.* (GH), *765* (G, P), *988* (P), *1110* (GH, US); above Orizaba, *Smyth 162* (US); *Müller s. n.*, *543* (NY), *148* (BR, NY); Zacuapan and vicinity, Barranca de Tenampa, *Purpus 2109, 3661* (Mo, US), *3058* (Mo, NY, UC, US); Mirador, *Liebmann 532* (US); Totutla, *Liebmann 509* (US). DATA INCOMPLETE: *Mohr s. n.* (US); *Linden Suppl. 47* (BR).

Triumfetta apetala has been treated thus far as a distinct species. I am convinced that it is the pistillate form of *T. Galeottiana*, as the younger fruiting specimens can be assigned to *T. Galeottiana* despite the fact that they have apetalous, pistillate flowers. I do not know of any mature fruiting specimen that could be included in *T. apetala* in opposition to *T. Galeottiana*.

43. Triumfetta heliocarpoides Bullock, in Kew Bull. 293. 1937. (T.: *Hinton 5159*).

Small shrubs 1.0–1.5 m. high; branches and inflorescence axes minutely stellate-tomentose. Leaves broadly ovate, usually 3-lobed, 10–15 cm. long and 7–9 cm. wide, the base subcordate to rounded, the tip gradually and narrowly acuminate, rather regularly and doubly serrate, the upper surface green, scabrous, very lightly pubescent with minute tufts of stellate hairs, the lower pallid, slightly more pubescent with prominent veins and veinlets; petioles long and slender, 5–10 cm. long, with short separate tufts of stellate hairs. Inflorescences gynodioecious, pistillate terminal, the cymes of 4–6 cymules, condensed in dense nodose clusters, the flowering peduncles 3–4 mm. long, the pedicels about 2 mm. long; flowers small, the bud about 3 mm. long slightly before anthesis, the apical appendages prominent though short; sepals oblong, 3–4 mm. long, densely but minutely tomentose without, glabrescent within; petals obovate, very small, only about 1 mm. long, the claw lightly plumose; gonophore 0.5–0.75 mm. long, the glands oblong, small, with ciliate upper margins; urceolus short, many-lobed, distinctly ciliate; staminodes 10, about 2 mm. long; ovary orbicular, the spinules about 25, recurved, the style about 1.5 mm. long, the stigma briefly 2-fid; hermaphroditic inflorescence not seen. Fruit orbicular, the body about 2 mm. in diameter at maturity, dark brown to black, glabrous, 3-loculate, usually 1 cell aborted, each 1-seeded, the spines 20–25, glabrous, 3–4 mm. long; seeds pyriform, small.

Known only from the state of México, usually growing at an altitude of about 1000 m.; flowering and fruiting from October to November.

Mexico: méxico: Ixtapan, Temascaltépec, alt. 1000 m., *Hinton 5159* (K, NY), *7001* (GH, K); Tejupilco, *Hinton 6779, 6780* (K).

Doubtful Species

1. Triumfetta calycina Turcz. in Bull. Soc. Nat. Moscou 36^1:574. 1863. (T.: Peru, *Mathews 889*).

A large-flowered species allied either to *T. speciosa* or *T. mollissima*. I have not seen the type, but the description fits *T. multilocularis*, except for the fact that *T. calycina* reportedly has only 15–16 stamens, whereas *T. mollissima* has 25–30.

2. Triumfetta Jelskii Szysz. in Rozpr. Akad. Umiejet. [Krakow], Mat.-przy. II, 9:224. 1895. (T.: Tambillo, Peru, *Jelski 280*).

A species allied to *T. caudata* according to the description. I have not seen the type and the description is inadequate for diagnosis.

3. Triumfetta brachypetala Urb. & Ekm. in Arkiv f. Bot. $23A^5$:80. 1930. (T.: Haiti, *Ekman H. 9462*).

A hybrid species between *T. Lappula* and *T. semitriloba*. I have not seen the type, and the very short description is inadequate for diagnosis.

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MISCELLANEA TAXONOMICA. I.

GRAMINEAE

SPOROBOLUS **hians** G. B. Van Schaack spec. nov. Gramen perenne usque ad 50 cm. altum. Culmi laxe fasciculati erecti 5–6-nodes, internodiis inferioribus brevissimis summo elongato et demum exserto. Foliorum inferiorum vaginae breves imbricatae valde striatae margine antrorse ciliato et ad apicem lateraliter barbatae caeterumque glabrae, summa glabra margine sparse pilosulo excepto; ligula ad seriem ciliorum usque ad .5 mm. longorum redacta; laminae inferiores planae 2–3 mm. latae usque ad 7 cm. longae in apicem tenuiter acutum gradatim attenuatae subtus laeves supra et margine scabridulae, superiores non visi. Panicula anguste pyramidalis usque ad 20 cm. longa et 10 cm. lata; rhachis gracilis inferne laevis superne antrorse minuteque scabra; rami praecipui capillares paullo flexuosi laeves vel minute scabri plerumque solitarii horizontaliter patentes, secundarii capillares patentes laxe spiculati; pedicelli laeves 1–3 mm. longi, terminali 3–5 mm. longo. Spiculae lanceolatae acutae 1.6–1.8 mm. longae in antheso hiantes purpureo-suffultae. Gluma inferior lanceolata .8 mm. longa obtusa erosa enervis hyalina, superior anguste ovata .9–1.0 mm. longa truncata erosa hyalina enervisque vel 1-nervis. Lemma lanceolatum vel ovatum 1.5–1.7 mm. longum acutum 1-nerve. Palea lemmati aequilonga acuta marginibus hyalinis. Antherae 1 mm. longae. Caryopsis non visus.—BRAZIL: MINAS GERAIS: S. Terezinha, Municipio Ituiutaba, Dec. 20, 1949, *A. Macedo 2045*. "Grass from 'Resfriado'." (Herb. Missouri Bot. Gard., HOLOTYPE).

Sporobolus hians resembles *S. pseudairoides* Parodi but differs from it in having shorter leaves, spreading panicle branches, a palea equalling the lemma in length and anthers 1 mm. long, the latter species having anthers only .25 mm. long.

LILIACEAE

HERRERIA **latifolia** Woodson, spec. nov. Frutex volubilis ramulis glabris glaucis sparse irregulariterque aculeolatis, internodiis ca. 15–18 cm. longis 2–3 mm. diametralis nodis incrassatis. Folia in rosulis oppositis sessilibus 6–7 sessilia obovato-elliptica apice breviter acuminata basim ca. tertia parte superiore versus gradatim angustata inter se plus minusve inaequalia 9–15 cm. longa 3–5 cm. lata membranacea utrinque glabra crebre multinervia. Inflorescentia per quamque rosulam unica paniculata vel pauciramosa 15–30 cm. longa, multiflora pedunculo glauco minute denseque hirtello vel basi glabrato; floribus luteolis, pedicellis ca. 2–3 mm. longis minute hirtellis, bracteis subtendentibus ovato-aculeatis subaequantibus, tepalis oblongo-ellipticis 3.5 mm. longis 2 mm. latis subaequalibus apice late acutis ibique minute papillatis caeterumque glabris basi in tubo campanuliformi ca. 1 mm. longo coalitis, filamentis staminum aciculiformibus 1.5 mm. longis glabris, antheris compresse ellipsoideis basi usque ad medium fissis 1.5 mm. longis, pistillo ampuliformi 3.5 mm. longo glabro.—BRAZIL: MINAS GERAIS: voluvel dos terrenos de pedra, S. Terezinha, Municipio Ituiutaba, Nov. 26, 1949, *A. Macedo 1317* (Herb. Missouri Bot. Gard., HOLOTYPE).

Issued September 30, 1950.

This certainly is the most handsome species of *Herreria* known at the present time. It is apparently most closely related to *H. Glaziovii* H. Lec. (*Glaziou 14,354* in hbb. Copenhagen and Missouri Bot. Gard.), which, however, has verticillate leaf-rosettes and clustered inflorescences with shorter, more branched, and glabrous peduncles.

VELLOZIACEAE

Vellozia **Macedonis** Woodson, spec. nov. Suffrutex subcaespitosus. Caudex subnullus simplex vel dichotome divisus foliorum emortuorum reliquiis tectus. Folia subradicalia lineari-aciculiformia 5–10 cm. longa medio ca. 2 mm. lata apicem obtusem gradatim attenuata basim versus gradatim ampliata vagina hyalina ca. 6 mm. longa 3 mm. lata fulvescentia margine proximate setoso-aculeolata caeterumque glabra multinervosa. Flores solitarii terminali longe pedunculati; pedunculo 6–8 cm. longo 3-gono 6-costato glabro; germine conico-campanulato indistincte 3-gono ca. 7 mm. longo, ostio ca. 5 mm. lato stramineo glabro laevi vernicoso margine obscure lobato; tepalis violaceis 6 oblongo-ellipticis acutis ca. 1 cm. longis 4–5 mm. latis; staminibus 18 in fasciculis 6 triplice convenitis, fasciculis tubo perianthii adnatis obtriangularibus tenuibus glabris exappendiculatis, filamentis et antheris subaequilongis sed medio in fasciculo paulo altius inserto cunctis ca. 5 mm. longis; stylo ca. 1 cm. longo, stigmate depresso-globoso ca. 1.5 mm. lato.—Brazil: minas gerais: mountains, alt. 1200 m., Ouro Preto, Jan. 7, 1950, *A. Macedo 2072* (Herb. Missouri Bot. Gard., holotype).

The habit of this species is reminiscent of *V. caruncularis*, although, of course, the latter has a densely tuberculate hypanthium. Our species appears to be most related to *V. graminea* Pohl, which, however, has strongly unequal stamens and elaborately appendaged phalanges.

LEGUMINOSAE

Pithecolobium **steyermarkii** Schery, spec. nov. Sect. Caulanthon. Arbor ramulis juventate brunneo-tomentulosis, prominente lenticellatis. Folia magna, pinniis 2-jugatis; petiolis brunneo-tomentulosis teretibus ca. 4 cm. longis, rhachibus aequalibus glande crateriforme sessile inter insertionem pinnarum inferiorum, rhachibus secondariis eglandulosis; foliolis oppositis 3–5-jugatis et una solitaria addita base extus, ovato-lanceolatis 4–8 cm. longis 15–30 mm. latis apice acuminatis basi late acutis, subtus leviter brunneo-tomentosis nervis prominentibus, supra glabris fuscioribus reticulatis; stipulis lanceolatis ca. 4 mm. longis. Inflorescentiae subfasciculatae cauliflorae brevi-spicate; floribus albis fragrantissimis sessilibus congestis subcapitatis, pedunculis 5–8 cm. longis brunneo-pubescentibus, bracteis ovatis parvis 1 mm. longis; calycibus cupuliformibus ca. 2 mm. longis brunneo-tomentosis brevi-dentatis, corollis tubulari-infundibuliformibus 8–9 mm. longis brunneo-tomentulosis brevi 5-dentatis, staminibus multis ca. 18 mm. longis tubo brevi exserto, ovariis lineari-oblongis, glabris, multiovulatis; fructu ignoto.—Ecuador: Prov. Santiago-Zamora, along Quebrada Honda, vicinity of Rancho Achupallas, alt. 2500–2700 m., *J. A. Steyermark* (Herb. Missouri Bot. Gard. type).

Pithecolobium steyermarkii

A tree with twigs, rachises and inflorescence brown-tomentulose; the leaves large, bipinnate, the pinnae 2 pairs and the leaflets 3–5 pairs plus a single basal leaflet to the outside on each pinna; the ovate-lanceolate leaflets opposite, short-petiolulate, relatively large (4–8 cm. long), pubescent (especially on veins) and light brown below, glabrous, darker and somewhat lustrous above; with 4 or 5 very prominent strongly arcuate lateral veins more or less confluent apexward a mm. or so from the margins, numerous smaller secondary and tertiary veins reticulate, the petiole bearing a single crateriform gland between insertion of the lower pinna pair, but it, the rachis and secondary axes otherwise eglandular. The congested or subfasciculate inflorescenses are borne on short spurs from the woody trunk; they are long-pedunculate, the floriferous portion very short-spicate (ca. 5 mm.) and thus appearing subcapitate. The congested, sessile, white flowers are described as very fragrant; the pubescent corolla is 4 to 5 times the length of the cupulate calyx, its teeth lanceolate, 1–2 mm. long, the tube about 7 mm. long; the ovary is turgid, symmetrical, glabrous.

The outstanding features of *P. steyermarkii* are the 2-jugate pinnae with relatively few and large leaflets, and the cauliflorous pedunculate inflorescences. A related species is apparently *P. ramiflorum* Benth., of Brazil, which, however, is said to have sessile spikes and larger leaflets.

ALBIZZIA **paucipinnata** Schery, spec. nov. Arbor 15 m. ramulis glabris longitudinaliter rugosis inconspicue lenticellatis. Folia magna bipinnata, pinnis 3–5-jugatis subopppositis; petiolis 3–5 cm. longis glabris supra subsulcatis glande parva conica vel subcrateriforme versus basem, rhachibus ca. 6–7 cm. supra sulcatis puberulis, axibus pinnarum ca. 6–8 cm. eglandularibus supra sulcatis puberulis; foliolis 7–12-jugatis oppositis inaequilateraliter oblongis 1–2 cm. longis 5–9 mm. latis, sessilibus, basi oblique rotundato-truncatis apice rotundatis et minute apiculatis, subtus puberulis supra glabris nitidis, costa aliquantum excentrica venis secondariis 3–4 paribus ascendentibus; stipulis nullis. Inflorescentiae terminales et subterminales axillares foliis aequilongae (ad 15 cm.) nodosae racemosae capitulis fasciculatis pedunculatis, pedunculis 1–pauci-aggregatis ca. 1 cm. longis tomentulosis, capitulis ca. 1 cm. diametro, bracteis lanceolato-cucullatis parvis pubescentibus; floribus albis odoratis multis congestis sessilibus, calycibus infundibuliformibus paene 2 mm. longis breviter et late 5-lobatis leviter puberulis, corollis infundibuliformibus ca. 3–4 mm. longis apice puberulis lobis ovate-lanceolatis prominentibus, staminibus multis (ca. 18) ca. 7 mm. longis tubo incluso, ovariis oblongis glabris turgidis multi-ovulatis; fructibus ignotis.—ECUADOR: Prov. El Oro, along Rio Amarillo upstream from Portovelo, alt. 640–760 m., *J. A. Steyermark 54035* (Herb. Missouri Bot. Gard. TYPE).

A large tree, the leaves bipinnate with few (3–5) pairs of subopposite pinnae, the pinnae with about 9 pairs of modest, sessile leaflets; the glabrous petiole moderately elongate and bearing a sessile gland basally, slightly exceeded by the eglandular rachis which is puberulent along the top side; leaflets inequilaterally oblong with a tendency toward being subfalcate, but rounded and minutely mucronulate apically, subtruncate basally, glabrous and lustrous above, puberulent below, the costa excentric but not marginal, the few lateral veins markedly ascending. The inflorescences arise from the upper axils as elongate nodose racemes of pedunculate heads that occur fasciculate from the rachial nodes; the peduncles are little more than 1 cm. long the heads (when dry) about 1 cm. in diameter. Flowers are small, funnelform, the corolla lobed for about 1/3 its length and about twice as long as the calyx; the staminal tube is included but about equalling the corolla.

The species is related to *Pithecolobium (Samanea) coripatense* Rusby [ALBIZZIA **coripatense** (Rusby) Schery n. comb.], from which it differs in being more glabrous, with somewhat longer flowers and inflorescences, and without glands on the pinnular rachis; and to *P. (Samanea) multiflorum* (HBK.) Benth., from which it differs in not having the leaflets falcate, glabrous, acute.

Cyathostegia (Benth.) Schery, gen. nov.

Swartzia, Sect. CYATHOSTEGIA Benth. in Benth. & Hook. Gen. Pl. 1:561. 1865.

Frutices *Swartziae* similes, calycibus cyathiformibus numquam irregulariter ruptis, leguminibus planis submembranaceis, bracteis persistentibus vel subpersistentibus, ovariis 1–2-ovulatis.

In working over Steyermark's Ecuadorean Leguminosae, Nos. 54839 and 54840, cursorily indicated by Dr. Steyermark as *Ateleia* (PAPILIONOIDEAE, SOPHOREAE), proved to belong to the section CYATHOSTEGIA of the genus *Swartzia* (CAESALPINOIDEAE, SWARTZIEAE). As nearly as can be told "ex char." they fall within the concept of S. *weberbaueri* Harms (in Fedde Rep. Sp. Nov. 18:235. 1922.). A check through the herbarium and literature on *Swartzia* made it apparent that both S. *mathewsii* Benth. (in Hook. Icon. III, 1:51, *pl. 1064.* 1870) and S. *weberbaueri*, apparently the only species of the section CYATHOSTEGIA, are quite untypical of *Swartzia*, and their inclusion there both inconvenient and misleading. It is therefore proposed to elevate the section CYATHOSTEGIA to generic rank, to become the genus *Cyathostegia* (CAESALPINOIDEAE, SWARTZIEAE) transitional from the CAESALPINOIDEAE to the SOPHOREAE of the PAPILIONOIDEAE. As such the genus is confined, as far as is known, to the Andean area of Brazil, Ecuador, Peru and probably Bolivia.

This genus is characterized, as is usually *Swartzia*, by unipetiolate flowers; many (about 30) stamens free or barely united at the base, the inner ones somewhat more slender and shorter, with large linear-oblong anthers; stiped ovary and (dehiscent) fruit; and slender style with small terminal stigma. However, the calyx is distinctly cyathiform or cupulate, subtruncate apically, not rupturing irregularly; the legume is flat and thin, never fleshy or turgid, one-seeded, exarillate, the valves thin and submembranous; the ovary is 1 to 2-ovulate, in contrast to the usually pluri-ovulate ovary characteristic of *Swartzia;* the bracts and bractlets are relatively persistent in contrast to the "very caducous" characterization of *Swartzia;* the stipe of the ovary is briefly adnate to the cupulate calyx below insertion of the petal and stamens; and the leaflets are more numerous than is often the case in *Swartzia.*

The species thus become **Cyathostegia matthewsii** (Benth.) Schery, n. comb. and **C. weberbaueri** (Harms) Schery, n. comb. The latter can be distinguished from the former by the longer, more lax inflorescense, the larger flowers and the smaller leaves. In *Steyermark 54839* the 1–3 lower flowers of the raceme that are in anthesis are strikingly larger than the several buds higher on the rachis. Both the large flowers and the small buds seem to be perfect and complete (although the style is not very evident in the buds), but the superficial appearance is that of a few perfect flowers below with staminate flowers above.

CASSIA **vargasi** Schery, spec. nov. Arbor?, ramulis flavo-tomentosis longitudinaliter substriatis, internodiis ca. 6 cm. longis. Folia magna 10–12-foliolata, stipulis ovato-lanceolatis ca. 7 mm. longis; petiolis ca. 2 cm. longis tomentosis

eglandularibus, rhachibus ca. 10 cm. longis flavo-tomentosis glande conico interpetiolulari inter jugem inferiorem foliolorum et frequenter inter alia juga; foliolis ovatis vel ellipticis, 2.5 (inferioribus)–8 (superioribus) cm. longis, 2–3 cm. latis apice late acutis base obtusis supra leviter pubescentibus subtus flavo-tomentosis, venis lateralibus ca. 8–10 paribus. Inflorescentia racemosa axillaris ca. 10 cm. longa; pedunculis ca. 7 cm. longis tomentosis; bracteis ovato-lanceolatis ca. 8 mm. longis subpersistentibus flavo-tomentosis; floribus aggregatis, pedicellis inferioribus ca. 3 cm. longis; sepalis inaequalibus ovatis vel orbiculari-oblongis 7–14 mm. longis longitudinaliter venosis glabris vel subglabris; petalis orbicularibus fere aequimagnis ca. 2 cm. longis conspicue venosis flavis glabris; staminibus 7, staminodiis 3, 4 antheris brevioribus ca. 6 mm. longis brevi-rostratis, filamentis 2–3 mm. longis, 3 antheris longioribus 7–9 mm. longis, filamentis 7–8 mm. longis fere erostratis; ovario lineari tomentoso stipitato turgido, stylo glabro, stigmate parvo; legumine ignoto.—PERU: CUZCO: Prov. Urubamba, Machupicchu, Feb., 1938, *C. Vargas C 985* (Herb. Missouri Bot Gard., HOLOTYPE).

By inference small tree or coarse shrub, yellow-tomentose throughout (older branchlets not seen); leaves large, 10- to 12-foliolate, the petiole and rachis markedly yellow-tomentose, bearing a black conic gland about 1 mm. long between the lower pair of leaflets and frequently the other pairs of leaflets as well; lower leaflets usually ovate and only ½ to ⅓ as long as the generally elliptic terminal leaflets, pubescent above and below, more heavily so (tomentose) and lighter in color below; inflorescence a long-pedunculate axillary raceme nearly equalling the leaf rachis, floriferous for about the terminal ¼ of its length, the conspicuous yellow-tomentose bracts subpersistent; pedicels of mature (lower) flowers elongate, the unopened buds (apexward) congested and sessile near the tip; sepals from the outermost inward becoming larger and more petaloid, essentially glabrous except the outermost lightly pubescent; petals large, short-clawed, glabrous, conspicuously venose; fertile stamens 7, glabrous, opening by paired but confluent terminal pores, the lowermost with a comparatively thin, elongate filament and a nearly erostrate, scarcely sagittate anther, the 2 median ones similar but with thicker, margined filaments and slightly larger anthers, the 4 upper ones with short, thick filaments and smaller, briefly rostrate anthers; staminodia 3–4 mm. long, obovate, flat, thin, the "blade" equalling the "claw"; ovary cinereous-tomentose, the style glabrous, the stigma terminal and inconspicuous.

This species falls near the well-known *Cassia (Adipera) tomentosa* L. f., from which it seems worthy of separation on the basis of the larger proportions in general, and the fewer and much larger leaflets. Possibly it grades into *Adipera santanderensis* Br. & Killip of Colombia, another variant of the *C. tomentosa* complex, but bears 5–6 rather than 4–5 pairs of leaflets and is decidedly more pubescent.

GALACTIA **pedunculata** Schery, spec. nov. Herba perennis subvolubilis tenuissima semiprostrata ca. 4 dm. longa, xylopodo ignoto sed ut videtur crassato; caulibus teretibus flexuosis subglabris vel minutissime appresso-strigillosis. Folia trifoliolata; stipulis anguste lanceolatis ca. 1.5 mm. longis; petiolis ca. 25 mm.

longis minute appresso-pubescentibus eglandularibus; foliolis linearibus 20–50 mm. longis et 3–6 mm. latis ad apicem obtusem angustatis ad basem rotundatis vel subcordatis supra glabris subtus leviter minuteque aureo-strigillosis et minutissime cinereo-lepidotis, venis lateralibus confluentibus prominente reticulatis, marginibus revolutis, petiolulis brevibus puberulentis, stipellis subulatis 1–1.5 mm. longis. Inflorescentia axillaris racemosa, pedunculis ca. 45 mm. longis; floribus paucis (ca. 5) terminaliter aggregatis vel subumbellatis purpureis, bracteis lanceolatis ca. 1.5 cm. longis, pedicellis 1–3 mm. longis pubescentibus; calycibus 5–6 mm. longis usque tertio inferiore pentapartitis lobis plus minusve aequimagnis ovato-lanceolatis acutis extus leviter aureo-puberulentis, vexillis orbicularibus ca. 12 mm. longis emarginatis glabris ad basem biauriculatis breve-unguiculatis, alis et carinis aequilongis subspatulatis ad basem auriculatis, staminibus glabris vexillo ad medium concrescenti, ovario plano pubescenti usque 10–15-ovulato, stylo glabro, stigmate parvo; legumine ignoto.—BRAZIL: MINAS GERAIS: on rocky terrain at about 1200 m., Ouro Preto (Saramenha?), Jan. 7, 1950, *A. Macedo 2070* (Herb. Missouri Bot. Gard., HOLOTYPE).

Slender, half-prostrate, vine-like herb to several dm., apparently perennial from a thickened rootstock; stems flexuous, minutely appressed strigose or subglabrous in age; leaves trifoliolate, stipulate, prominently petiolate; leaflets linear (in a few first-formed, basal leaves linear-lanceolate), gradually contracted to a blunt and briefly mucronate apex, glabrous above, scatteringly golden-strigulose below and minutely cinereous-scurfy, the costa prominent, depressed above but elevated below, the lateral venation markedly reticulate; inflorescence a very contracted head-like or umbel-like axillary raceme (or condensed panicle?), floriferous for the upper few mm. with a few short-pedicellate flowers but conspicuously pedunculate below, the peduncle almost twice the length of the petioles; flowers moderate, the calyx prominently 5-lobed, the corolla about 12 mm. long; stamens equalling the corolla, fused for at least half their length, the alternate filaments somewhat unequal; anthers versatile, elliptic, less than 1 mm. long, with a dark connective; ovary linear, pubescent (especially marginally), flattened; style glabrous, arcuate, comparatively stout and terminating abruptly as an unexpanded, glabrous stigma.

This species is similar to *G. linearifolia* Hoehne, known from São Paulo, Brazil. It is one of a very few species centering around the rather unique *G. gracillima*. *G. pedunculata* differs from both *G. gracillima* and *G. linearifolia* in the conspicuously pedunculate inflorescences. The vine-like habit and unusual, slender leaflets serve to distinguish it from most other species of *Galactia*. The genus is regarded as generally having the vexillar stamen free. This is not true of *C. pedunculata* nor its near relatives.

VIOLACEAE

RINOREA **roureoides** Woodson, spec. nov. Arbor ca. 7 m. alta; ramulis graciliusculis glabris. Folia alternata obovato-elliptica subcaudato-acuminata basi obtusa vel late acuta apicem versus indistincte crenulata ca. 7–12 cm. longa ca.

2.5–5.0 cm. lata firmiter membranacea utrinque opaca glabra prominente venosa; petiolis ca. 5 mm. longis glabris. Inflorescentia paniculata in axillis foliorum superiorum fasciculata rariusve solitaria; pedunculis ca. 4–7 cm. longis gracilibus minute papillatis, ramulis inferioribus 3–5-floris superioribus saepissime 1-floris, bracteis minimis anguste lanceolatis. Flores albi; pedicellis ca. 2 mm. longis minute papillatis; calycis laciniis aequalibus ovato-deltoideis late obtusis 3-nerviis ca. 1 mm. longis minute ciliolatis; petalis late oblongis ca. 3 mm. longis ciliolatis; staminum filamentis ca. 1 mm. longis basi glandula reniformi minute emarginata ca. 0.5 mm. longa adnata, antheris subquadratis ca. 0.5 mm. longis, appendicibus apicalibus latissime ovatis obtusis laceratis ca. 1 mm. longis hyalinis brunneis. Pistilli ovarium globosum ca. 1 mm. diam. glabrum, ovulis 3; stylo ca. 2 mm. longo. Capsula globosa ca. 5 mm. diam. glabra.—PANAMA: COLON: Río Viejo, vicinity of Puerto Pilon, alt. 10 m., Feb. 2, 1947, *P. H. Allen 4099* (Herb. Missouri Bot. Gard., HOLOTYPE).

The fascicled inflorescences characterize this species, which resembles *Rourea glabra* superficially.

CARICACEAE

JACARATIA **dolichaula** (Donn. Sm.) Woodson, comb. nov.

Carica dolichaula Donn. Sm. in Bot. Gaz. 23:247. 1897.

This species exhibits the antesepalous corolla lobes, circumscissile calyx, caudate anthers, and laminately 5-lobed stigma of *Jacaratia*, as well as the palmately compound leaves.

LOGANICACEAE

SPIGELIA **aceifolia** Woodson, spec. nov. Fruticulus ca. 1 dm. altus e radice lignoso subtuberoso; ramis gracilibus teretibus inferne pauci-ramosis superne simplicibus dense minute pilosulis. Folia omnino opposita sessilia vel subsessilia trigonalia apice minute mucronata basi truncata vel obscurissime cordata 5–7 mm. longa basi 2.5–3.0 mm. lata coriacea margine valde revoluta supra glabra subtus minute pilosula. Flores in axillibus foliorum superiorum solitarii sessiles; calycis laciniis lineari-lanceolatis subsetosis 5 mm. longis glabris; corolla infundibuliformi rosea extus glabra, tubo proprio cylindraceo ca. 5 mm. longo, faucibus conicis ca. 3 mm. longis, ostio ca. 2.5 mm. diam., lobis oblongo-ovatis acutis ca. 5 mm. longis; staminibus in faucibus corollae inclusis, antheris ca. 1.5 mm. longis. Fructus ignotus.—BRAZIL: MINAS GERAIS: Serra do Cipó, Municipio Jaboticatubas, campo-margem est. rodagem, frequencia pouco, March 29, 1949, *M. Magalhaes 4,445* (Herb. Missouri Bot. Gard., HOLOTYPE).

Closely related to *S. stenophylla* Prog., which is glabrous and larger in all respects.

APOCYNACEAE

MANDEVILLA **ligustriflora** Woodson, spec. nov. Frutex volubilis; ramulis teretibus glabris maturitatem cortice rubro-brunneo striato atque lenticellato.

Folia opposita petiolata oblongo-elliptica subcaudato-acuminata basi obtusi 5–7 cm. longa 2.0–2.5 cm. lata coriacea omnino glabra supra nervo medio basi pauciglanduligero subtus pallidiora venis utrinque immersis nervo medio excepto; petiolis 0.5–1.0 cm. longis. Inflorescentia axillaris umbelliformis pauciflora; pedunculo ca. 1.5 cm. longo; bracteis lineari-lanceolatis minimis; pedicellis ca. 1 cm. longis; calycis laciniis ovatis obtusiusculis ca. 1.5 mm. longis scariaceis extus minute papillatis intus in margines pauciglanduligeris; corolla infundibuliformi pro genere parvissima extus rubro-tincta atque minute puberulo-papillata intus viridi, in alabastro rotundate ovoidea haud apiculata tubo proprio ca. 2 mm. longo basi ca. 1 mm. diam., faucibus tubulo-campanulatis ca. 3 mm. longis, ostio ca. 1.5 mm. diam., lobis ovatis ca. 1 mm. longis; antheris oblongo-sagittatis basi obtuse 2-lobatis dorso glabris; pistillo carpellis ovoideis glabris, nectariis 5 compresse oblongoideis ca. 1 mm. longis ovarium paulo superantibus; stigmate umbraculiformi ca. 2 mm. longo longe apiculato.—ECUADOR: Zamora-Huaico, ca. 6 km. s. e. of Loja, alt. 2300–2400 m., July 3, 1947, *R. Espinosa 1547* (Herb. Missouri Bot. Gard., HOLOTYPE).

This species approaches *M. jasminiflora* very closely indeed. The latter species, however, has narrower leaves with veins prominently elevated beneath and sunken above, and somewhat smaller corollas which are glabrous and conspicuously apiculate in the bud.

This occasion may be taken to confess that my description of *M. jasminiflora* (Woods. in Ann. Missouri Bot. Gard. 28:273. 1941) seriously errs in the description of the leaves as glandular the length of the midrib and of the calyx lobes as bearing a single opposite squamella, which together prompted me to place the species in the subgenus *Exothostemon* rather than in *Eumandevilla* where it actually belongs.

MANDEVILLA **Espinosae** Woodson, spec. nov. Frutex volubilis; ramulis crassiusculis dense ferrugineo-tomentulosis maturitate bene corticosis. Folia opposita brevissime petiolata late ovato-elliptica anguste acuminata basi cordata auriculis rotundatis convergentibus, 8–14 cm. longa 5–8 cm. lata membranacea supra sparsiuscule hirtella nervo medio basi pauciglanduligero subtus dense ferrugineo-tomentulosa; petiolo ca. 5 mm. longo. Inflorescentiae in axillas alternatas foliorum racemiformes pluriflores; pedunculis ca. 7–10 cm. longis dense ferrugineo-tomentulosis; bracteis minimis; pedicellis 1.0–1.25 cm. longis; calycis laciniis ovato-lanceolatis acuminatis 4–5 mm. longis extus ferrugineo-puberulis intus in margines pauciglanduligeris; corolla infundibuliformi viridi-gilva extus glabra; tubo proprio ca. 2 cm. longo basi ca. 1.5 mm. diam., faucibus late conicis ca. 7–8 mm. longis ostio ca. aequilato, lobis oblique obovatis ca. 3 cm. longis patulis; antheris oblongo-sagittatis basi minute emarginatis 8 mm. longis dorso glabris; pistillo carpellis oblongo-ovoideis ca. 2 mm. longis sparse minuteque pilosulis, cum nectariis 5 compresse ovoideis ca. dimidio aequantibus; stigmate umbraculiformi 3 mm. longo longiuscule atque anguste apiculato.—ECUADOR: Yacubiño (Zarumalado occidental de Chilchiles), alt. 2250 m., Sept. 3, 1947, *R. Espinosa 2077*

(Herb. Missouri Bot. Gard., HOLOTYPE).

Apparently most closely related to *M. glandulosa,* but differing conspicuously in the shallow, conical corolla throat.

MANDEVILLA **tricolor** Woodson, spec. nov. Frutex volubilis; ramulis parvis minute puberulis adultis crassiusculis cortice luteo-brunneo striato bene lenticellato. Folia opposita longiuscule petiolata oblongo-elliptica breviter acuminata basi late obtusa vel rotundata 2–4 cm. longa 0.8–1.5 cm. lata membranacea supra glabra nervo medio sparse puberulo excepto ibique basi pauciglanduligero subtus in axillas nervo medio inconspicue pilosula caeterumque glabra; petiolis 4–6 mm. longis minute puberulis. Inflorescentiae in axillas alternatas foliorum corymbiformes pluriflores; pedunculis ca. 1 cm. longis minute puberulis; bracteis 3–4 mm. longis subfoliaceis; pedicellis ca. 1.5 cm. longis minute puberulis; calycis laciniis oblongis vel oblongo-ellipticis acutis plus-minus inaequalibus 5–6 mm. longis foliaceis margine revolutis extus-intus sparse pilosulis intus cum squamellis ligularibus numerosis cinctis; corolla salverformi, tubo 1.0–1.2 cm. longo basi ca. 2 mm. diam. albo extus minute puberulo-papillato, lobis oblique obovatis ca. 6 mm. longis patentibus purpureis extus intusque puberulo-papillatis; antheris in tubi medio inserto anguste oblongis basi paulo concavis 4 mm. longis dorso glabris; pistillo carpellis obovoideo-oblongoideis glabris ca. 1 mm. longis squamellis 5 brevioribus; stigmate umbraculiformi ca. 2.5 mm. longo longe apiculato.—ECUADOR: Las Chinchas, 64 km. west of Loja, alt. 1700 m., March 1, 1947, *R. Espinosa 1332* (Herb. Missouri Bot. Gard., HOLOTYPE).

Apparently mostly closely related to *M. scutifolia,* and differing from it chiefly in the smaller leaves and very conspicuous, foliaceous calyx.

HOLALAFIA **Schumannii** (Stapf) Woodson, comb. nov.

Alafia Schumannii Stapf, in Fl. Trop. Afr. 4^1:197. 1904; Hutchinson & Dalziel, Fl. W. Trop. Afr. 2^1:45. 1931.

I have chanced upon the need for this new combination while identifying a few of Dr. J. T. Baldwin's plants of West Africa. An isotype of *Alafia Schumannii* (*Zenker 1662* in Herb. Missouri Bot. Gard.) shows not only the syncarpous ovary but the distinctive inflorescence structure of *Holalafia.* Incidentally, one of Dr. Baldwin's plants is a fruiting *Holalafia multiflora* Stapf: the follicles are linear, nearly 8 dm. long and about 1.5 cm. thick, and glabrous; the seeds have a body about 2.5 cm. long, the coma (with yellowish hairs about 6 cm. long) borne along a rostrum 1.5 cm. long, much as in *Funtumia,* but the hairs spreading and not retrorse (*Baldwin 13969* in Herb. Missouri Bot. Gard. and U. S. Dept. Agr.). I have never seen *Holalafia* and *Alafia* distinguished on the basis of seeds, but I suspect that in the former genus the coma may always be rostrate and in the latter sessile.

ASCLEPIADACEAE

MATELEA **Meyeri** Woodson, spec. nov. Frutex volubilis; ramulis gracilibus complicate pubescentibus (sparsiuscule eglandulo-pilosis cum trichomis brevioribus

plus minusve densioribus tum simplice eglandulosis tum brunneis bulbosis glandulosis interspersis). Folia opposita petiolata, lamina ovata cordata acuminata 8–9 cm. longa 4.5–5.0 cm. lata membranacea utrinque puberula (praecipue eglandulosa); petiolo ca. 3 cm. longo ut in ramulo vestito. Inflorescentia corymbiformis pluriflora; pedunculo ca. 1–2 cm. longo cum pedicellis ut in ramulo vestito; pedicellis gracilibus ca. 1.5 cm. longis; bracteis lineari-lanceolatis ca. 0.2 cm. longis. Flores ut creduntur gilvi extus plus minusve complicate pubescentes; calycis laciniis ovato-lanceolatis acuminatis ca. 0.3 cm. longis; corollae rotato-campanulatae tubo ca. 0.2 cm. longo basi ca. 0.1 cm. diam., faucibus ca. 0.2 cm. diam., lobis lineari-lanceolatis acuminatis erectis vel ascendentibus ca. 1 cm. longis; corona ample infundibuliformi carnosa corollae tubae valde adnata ostio ca. 3 mm. diam., sat integra sed obscure 5-loba quoque ligulam brevem gerente intus omnino carunculata; gynostegio brevi-stipitato ca. 1 mm. alto late 5-gono ca. 2 mm. diam., stigmate depresso, polliniis horizontalibus falciformi-subpyriformibus cum caudiculo breve ca. 0.5 mm. longis. Folliculi immaturi conspicue muricati dense complicate pubescentes.—MEXICO: TAMAULIPAS: open places along Río San Marcos, 5 mi. west of Ciudad Victoria, alt. 500 m., June 13, 1948, *F. G. Meyer & D. J. Rogers 2500* (Herb. Missouri Bot. Gard., HOLOTYPE).

A most curious species, obviously referable to my subgenus *Heliostemma* (cf. Ann. Missouri Bot. Gard. 28:221. 1941), but superficially very similar to *Matelea belizensis* (subgen. *Tiarastemma*).

MATELEA **Rogersii** Woodson, spec. nov. Frutex volubilis; ramulis gracilibus complicate pubescentibus (sparsiuscule eglandulo-pilosis cum trichomis brevioribus plus minusve densioribus tum simplice eglandulosis tum brunneis bulbosis glandulosis interspersis). Folia opposita longe petiolata, lamina late ovata cordata abrupte acuminata 15–20 cm. longa 13–15 cm. lata membranacea utrinque complicate puberula; petiolo ca. 6–7 cm. longo ut in ramulo vestito. Inflorescentia subumbelliformis pluriflora; pedunculo ca. 7–8 cm. longo cum pedicellis ut in ramulo vestito; pedicellis 2.5 cm. longis crassiusculis; bracteis anguste lanceolatis ca. 0.4 cm. longis. Flores virescentes; calycis laciniis elliptico-suborbicularibus obtusis subfoliaceis 0.7–0.8 cm. longis extus complicate pubescentibus; corolla late rotata eliganter reticulo-venosa extus intusque indistincte papillata ca. 2.5 cm. diam., lobis late ovato-deltoideis rotundatis minuteve mucronulatis ca. 0.8–1.0 cm. longis 1.3 cm. latis patulis; corona disciformi corollae faucibus adnata ca. 3 mm. diam., integra vel indistincte irregulariterque crenulata; gynostegio sessile ca. 1 mm. alto latissime 5-gono ca. 3 mm. diam., stigmate sat plano, polliniis horizontalibus subtriangulari-pyriformibus cum caudiculo late alato subaequilongo ca. 1 mm. longis. Fructus desunt.—MEXICO: NUEVO LEON: in arroyo, near Dulces Nombres, alt. 1400 m., Aug. 23, 1948, *F. G. Meyer & D. J. Rogers 3072* (Herb. Missouri Bot. Gard., HOLOTYPE).

A member of subgen. *Eumatelea* sect. *Reticulatae*, closely allied to *M. reticulata* and *M. Gentlei*, but differing from both in the much larger flowers, the large, suborbicular calyx lobes, and the nearly entire corona disc.

MATELEA **ionantha** Woodson, spec. nov. Frutices volubiles; ramulis gracillimis juventate minute pilosulis maturitate cortice sulcato dilute luteo tectis. Folia opposita longe petiolata, lamina ovata profunde cordata sensim acuminata 5–7 cm. longa 2.5–4 cm. lata membranacea utroque pagina sparsiuscule pilosula margine densius ciliolata, petiolo 2–2.5 cm. longo. Inflorescentia lateralis umbelliformis pauciflora, pedunculo 1–1.5 cm. longo, pedicellis ca. 5 mm. longis minute pilosulis cum glandulis minutissimis fuscis interspersis, bracteis minimis. Flores parvi purpurei, calycis laciniis ovato-lanceolatis acuminatis 4–5 mm. longis complicate pubescentibus, corolla rotato-subcampanulata extus intusque dense complicate pubescente ca. 1.5 cm. diam., lobis ovatis obtusis 5–6 mm. longis, patulis; corona annulata carnosa corollae faucibus valde adnata, segmentis 5 paene coalitis rhomboideis ca. 0.5 mm. altis 1 mm. latis planis dente truncato ca. 1 mm. alto excepto per saepto angusto ad gynostegio junctis. Gynostegium fere sessile ca. 2 mm. diam., stigmate depresso ca. 1.5 mm. diam. cum umbone lato, antherarum appendicibus apicalibus brevissimis, polliniis brevissime arcuatis fere quadratis ca. 0.3 mm. longis et latis margine superiore pellucido, caudiculis corpusculoque minimis.—MEXICO: VERA CRUZ: over shrubs at edge of oak forest near El Puerto, above Acultzingo, alt. 7600–7800 ft., Sept. 13, 1944, *A. J. Sharp 44,830* (Herb. Missouri Bot. Gard., HOLOTYPE).

Referable to subgen. *Heliostemma* (cf. Ann. Missouri Bot. Gard. 28:233. 1941), this species apparently is most closely allied to *M. cyclophylla* (Standl.) Woods., but differs in the vastly different foliage and smaller flowers with pollinia so short as to be scarcely arcuate.

MARSDENIA **Rotheana** Woodson, spec. nov. Sect. ELLIPTICARUM Rothe. Frutex volubilis; ramulis glaberrimis maturitate cortice singulare suberoso-fimbriatis. Folia modice petiolata, lamina ovato- vel oblongo-elliptica abrupte breviterque acuminata basi truncata vel plus-minus cordata 6–8 cm. longa 2.5–4.0 cm. lata firmiter membranacea glaberrima subtus pallidiora; petiolis 0.7–1.0 cm. longis sparse appresse pilosulis. Inflorescentia lateralis umbelliformis pauci- (plerumque 3-) flora; pedunculo ca. 0.5 cm. longo; pedicellis filiformibus 1.5–2.0 cm. longis glaberrimis; calycis laciniis ovatis obtusis vel rotundatis ca. 2 mm. longis minute ciliolatis intus cum squamellis minutis alternatis 1–2; corolla campanulato-rotata extus intusque glaberrima lutea, tubo ca. 2.5 mm. alto faucibus ca. 6 mm. diam., lobis late ovato-trigonalibus late acutis ca. 6 mm. longis patulis. Gynostegium dimidio exsertum ca. 4 mm. longum; stigmate late conico; coronae squamis duplicibus dorso subquadratis ca. 2 mm. longis et latis processu aciculari paulo breviori. Fructus ignoti.—PANAMA: COCLÉ: Cerro Pajita, region north of El Valle de Antón, alt. 3500 ft., May 12, 1947, *P. H. Allen 4495* (Herb. Missouri Bot. Gard., HOLOTYPE).

This is the first species of Rothe's section ELLIPTICAE (cf. Engl. Jahrb. 52:424. 1915) to be described from the continent. Its closest relative would appear to be *M. Dussii* Schltr. of Martinique, which has smaller, reddish flowers with much shorter pedicels.

SOME AMERICAN CARBONIFEROUS FERN FRUCTIFICATIONS[1]

SERGIUS HARRY MAMAY[2]

Introduction

Prior to the discovery of coal balls and the development of techniques which made possible the cutting of petrifactions for detailed anatomical studies, the attention of paleobotanists was mostly limited to considerations of impressions and compressions. The resultant early studies demonstrated that certain plants which bore fern-like foliage, often preserved in exquisite fashion, constituted conspicuous elements in the Coal Age floras of Europe and America. To Adolph Brongniart falls the bulk of the credit in the nomenclature of these foliar compressions.

At an early date fertile specimens bearing circular groups of sporangia upon the lower surfaces were found among the fern-like leaf impressions. Such specimens, the majority of which were referable to the genus *Pecopteris*, were, by virtue of what information could be gathered from the compressed fructifications, commonly regarded as constituting a marattiaceous element in the Coal Age floras. This opinion met with little controversy until the early part of the 20th century, when it was demonstrated that at least some of the Carboniferous plants to which fern-like foliage was attributed bore seeds. This initiated our knowledge of the pteridosperms, an extremely interesting group which has since been much investigated. While some authors preferred to look with doubt upon the marattiaceous affinity of the pecopterid fructifications, the striking anatomical similarity of the fossil stem *Psaronius* to the living marattiaceous genus *Angiopteris*, along with other factors, appeared to strengthen the validity of the Carboniferous Marattiaceae, despite the supposed likenesses between the pecopterid fructifications and certain of the pteridospermous microsporangiate fructifications.[3]

Anatomical studies of coal ball plants, begun in England in 1868 by Binney and further pursued by such outstanding anatomists as Williamson and Scott, demonstrated the presence of an additional complex in the Carboniferous floras, the primitive ferns or Coenopterideae (Seward, 1910). Although these plants are yet incompletely known, the nature of their vascular systems and fructifications indicates affinities with certain of the ferns rather than with other vascular cryptogams.

In spite of the fact that investigations of coal balls in America have been under way for only two decades, we have achieved at least an introductory picture of our Coal Age floras. Numerous coal ball localities have been discovered in Illinois, Iowa, Indiana, and Kansas, with the result that significant literature has accumu-

[1] An investigation carried out in the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor in Philosophy at Washington University. This study was aided by a grant from the Penrose Fund of the American Philosophical Society.

[2] John Simon Guggenheim Fellow, University of Cambridge, England, 1950-51.

[3] This problem is considered in greater detail in the summary.

lated.[4] It is known that American Carboniferous floras contained liberal representatives of the Marattiaceae, Pteridospermae, and Coenopterideae, and while considerable attention has been directed toward studies of the anatomy and fructifications of the American pteridosperms, much remains to be learned about the Marattiaceae and Coenopterideae, chiefly from the standpoint of their fructifications. A few brief descriptions of the vegetative organs and fructifications of these plants have been published, yet their abundance in recent collections indicates that this represents only a beginning toward a comprehensive knowledge of these elements of the American floras.

The scarcity of literature dealing with petrified fructifications might be explained thus: The organs in question are extremely small and rarely occur in sufficient quantities to constitute conspicuous masses. The better-known descriptions have been based chiefly on remarkably large aggregations of fructifications such as *Botryopteris forensis* Renault and *B. globosa* Darrah. Such specimens are rare. To undertake a study of these organs involves painstaking systematic inspections of many petrifactions under reasonably high magnification, a process which might easily be deferred in favor of investigation of larger, more conspicuous stems, seeds, etc.

The present paper treats the various fructification species present in coal balls from various American localities. These have been critically compared with descriptions of all related species from both Europe and America, with the result that several distinctly new entities are recognized. These include three new species of *Botryopteris* Renault; one new species of *Cyathotrachus* Watson, the generic concept of which is emended; three new species of *Scolecopteris* Zenker, and a new variety of *S. minor* Hoskins, in addition to an emendation of and supplementary data concerning *S. latifolia* Graham; and a new genus, *Eoangiopteris*, which is postulated as a progenitor of the *Angiopteris* type of modern marattiaceous sori.

In recognizing new species, the size of sporangia, structure of sporangial walls, and the number of sporangia in the fructifications are carefully considered as criteria, with critical attention given to the range of variation which might be expected within the limitations of a species. Where possible, details of the supporting pinnules are also noted. All these features appear to be trustworthy criteria for speciation, but it has been found that the spores present the single outstandingly dependable basis for comparison. While variation among the spores of the various species of a given genus is extreme, from the standpoints of both size and morphology (the spores of *Scolecopteris*, for instance, range from 10 to 80 μ in diameter, and may be of either bilateral or tetrahedral symmetry), they are remarkably constant among different specimens of a given species[5]; considering the spores together with the other variables mentioned above, a reliable concept of the species complex of a fructification genus may be arrived at.

[4] A comprehensive review of American coal ball literature, is being prepared by H. N. Andrews, for a future number of the 'Botanical Review.'

[5] In limiting the diagnostic value of these spores to the specific level we concur with Knox (1938) who wrote: ". . . and even for genera there are not many examples where spore characters could be held to be diagnostic."

The accepted practice of designating holotypes in describing new species of fossil plants is hardly practicable when dealing with fructifications as small as those involved in this study. With a stem specimen of a centimeter or so in diameter and several centimeters in length, it is possible to make sufficient sections to gain a thorough understanding of the specimen and still preserve enough material to constitute a holotype for future reference. However, the fructifications described in this paper scarcely exceed a single millimeter in length, making it impossible to arrive at a reconstruction from a single specimen. Fortunately, their smallness is generally compensated for by their abundance in the coal balls. In several cases, the initial cut of a coal ball has exposed numerous fructifications sectioned in all planes and levels. Thus we have been able to obtain a complete and accurate concept of the nature of a fructification species by examination of a single peel. In more critical studies of exceptional specimens, however, serial peel sections were employed. Since the descriptions of new species are based upon not one but several specimens, we will cite *syntypic* slides which have been made from peels selected because of their abundant fructification content or excellence of preservation, or both.

Materials and Techniques

At the beginning of this investigation, attention was concentrated on a collection of coal ball slabs from the Urbandale Mine near Des Moines, Iowa, particularly rich in fern fructifications, and it was in them that the majority of the specimens described were found. This material was generously donated to the Washington University collection by Mr. Frederick O. Thompson of Des Moines, whose collecting activities during the past several years have indeed proven a boon to recent American paleobotanists.

As the investigation proceeded, coal balls from various other localities were collected and inspected. Those which have produced fructification material are:

1. The Urbandale Mine, located 1.2 miles west of Des Moines, Iowa, on U. S. Highway #6 (Walnut Township, Dallas County). This coal lies in the Des Moines Series of the Pennsylvanian. (See Andrews and Kernen, 1946.)

2. Berryville, Illinois. This small outcrop, which is found in a stream bed approximately 2 miles northeast of Berryville, Illinois (Sumner Quadrangle, Lawrence County), lies in the upper portion of the McLeansboro Group of the Pennsylvanian of Illinois.

3. Big Creek #1 Mine of the Wasson Coal Mining Corporation, which is located approximately 2 miles south and 1.5 miles east of Lynnville, Indiana. This coal (Petersburg V) lies in the upper portion of the Des Moines Series.

4. Strip pits of the Pittsburgh and Midway Coal Company, located 4 miles south of Mineral, Kansas (Columbus Quadrangle, Cherokee County). This coal is known as the Fleming Coal, and lies in the upper one-third of the Cherokee Shale, which is found in the Des Moines Series of the Pennsylvanian.

5. Shore, Lancashire, England. The material from this locality consists of a single small coal ball fragment. This coal seam lies in the Great Coal Ball Horizon of the Lanarkian Series. (See Schopf, 1941.)

While each of these localities has produced fern fructifications in some abundance, none has approached the Urbandale for the number of species present. However, at the time of this writing, the Mineral, Kansas, material is only beginning to be investigated, but it promises to equal or even surpass the Urbandale locality in diversity of the flora.

The peel technique followed is essentially that outlined by Pannell (1942). In a few instances it was necessary to make successive peels at intervals as close as possible, due to the smallness of the specimens. Those specimens selected for illustrative purposes were cut from the peel, mounted in Clarite on glass slides, and photographed with Panatomic X sheet film and a green Wratten filter.

All the slides cited are catalogued in the Washington University paleobotanical collection.

COENOPTERIDALES

While much is known of the vegetative anatomy of the coenopterids, or primitive ferns, relatively little is known of their fructifications. The various genera are easily distinguished on the basis of their petioles, which exhibit great diversity of structure, in contrast to the generally simple and uniform organization of the stems. Although considered to be an extremely primitive group of vascular plants, they nevertheless embrace genera with certain structural modifications suggestive of higher groups, e. g., the axillary branching of *Ankyropteris*, the weak but distinct secondary thickening in the stem of *Botrychioxylon*, and the compact, synangial fructifications of *Chorionopteris*, which were borne on well-developed laminae.

Regarding the fructifications, the diversity of structure within the coenopterids is great. In the most primitive representative, *Stauropteris*, the sporangia are solitary, exannulate, massive-walled, and borne terminally on the ultimate ramifications of the radially symmetrical "frond." Between this extreme and that seen in *Chorionopteris*, various intermediate forms are known (this series is considered more critically in the conclusion of this paper). The extremely diverse structure of the petioles, the axillary branching, and the cambial activity, prompt the conclusion that the coenopterid ferns must have constituted an extremely plastic evolutionary plexus from which several lines of fern (and probably pteridosperm) development began to emerge early in the history of vascular plants. The appearance in the late Paleozoic of fern fructifications which show strong affinities with the Schizaeaceae *(Senftenbergia)*, Gleicheniaceae *(Oligocarpia)*, and Marattiaceae *(Scolecopteris, Cyathotrachus*, etc.), along with stem remains whose anatomy indicates osmundaceous affinity *(Thamnopteris, Zalesskya)*, appears to strengthen such a supposition. This would also seem to imply an extremely early differentiation of both the eu- and leptosporangiate development of fructifications, very

likely much earlier than the development of laminate foliar organs.

The vegetative remains of several coenopterid genera have been reportéd in American paleobotanical literature.[6] Stems and petioles of *Ankyropteris, Botryopteris, Etapteris, Stauropteris, Anachoropteris,* and *Grammatopteris*[7] have been reported in America. However, only the genus *Botryopteris* is known from its fructifications, these having been reported by Darrah (1939) and Graham (1935). Graham also described a new fructification genus of apparently coenopterid affinity, but which has not been correlated with any stem genus *(Notoschizaea robusta)*. He pointed out a strong resemblance of *Notoschizaea* to the fructification *Corynepteris,* however.

The coenopterid fructifications found during this investigation are representatives of the genus *Botryopteris* Renault, the vegetative organs of which are found in some abundance in American coal balls. The history of the fructification species of *Botryopteris* follows:

BOTRYOPTERIS Renault, Ann. Sci. Nat. (Bot.) VI, 1:223–229. 1875.

Renault's type species, *B. forensis,* was based upon silicifications from the Permo-Carboniferous of Autun and St. Etienne. Renault was fortunate in finding both the vegetative organs and the fructifications, with no reason for doubt as to the correlation between the two. The sporangia were produced in small clusters on the termini of the ultimate ramifications of a much-branched "frond," resulting in a large compound fructification containing possibly several thousands of sporangia. The individual sporangia are shortly pedicellate, more or less pyriform, and attain lengths of 2 mm. and diameters of 1 mm. The sporangial walls are, according to Renault, ". . . . formées d'un seul rang de cellules polyédriques . . .", and are distinctive in possessing a multiseriate annulus-like band of enlarged cells which extends from the apex to the base along one side of the sporangium. Dehiscence occurred by a longitudinal cleft along the thin opposite wall. The spores are spherical, apparently smooth-walled, and attain diameters of 70 μ.

In the same publication Renault described a second species of *Botryopteris (B. dubius)* which he later transferred to the genus *Zygopteris*.

Scott (1910) described a group of sporangia from the Lower Carboniferous of Pettycur, which was found in intimate association with a petiole of *B. antiqua*. The sporangia measure from 240 to 280 μ in diameter, with the cells of the annulus reaching 60 μ in diameter. The spores average 25 μ in diameter, and are somewhat triangularly flattened. A structure which he interpreted as of possible indusial nature was found associated with the sporangia. Scott (1920) has also reported similar small botryopterid sporangia in association with the Lower Carboniferous species *B. hirsuta* and *B. ramosa*.

Graham (1935) described botryopterid petioles and sporangia from the Upper Pennsylvanian of Illinois, naming them *B. americana*. Among the fructifications

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[6] Darrah (1941) has summarized the American coenopterids.

[7] An excellent specimen of *Grammatopteris* has only recently been found by us in a coal ball from Berryville, Illinois. This is apparently the first known occurrence of this genus in this country.

he noted "sterile" sporangia which he termed "specialized" without further elaboration. Dimensions are not cited, but judging from the size of the drawings and the magnifications given the sporangia appear to be approximately .70 mm. wide and 1.30 mm. long, with spores about 30 μ in diameter.

The second American species, *B. globosa* Darrah (1939), is from the Upper Pennsylvanian of Iowa. This remarkable fructification is the American counterpart of Renault's *B. forensis*, consisting of innumerable sporangia borne in terminal tufts on a highly branched "frond."

During the present investigation *Botryopteris* fructifications have been found in coal balls from the Urbandale Mine, Iowa, and Berryville, Illinois. These are much smaller than previously described species, with the exception of those reported by Scott. Although they do not differ greatly among themselves in sporangial dimensions, three distinct species are recognized, based chiefly on spore morphology.

BOTRYOPTERIS **fecunda**, sp. nov. (figs. 1–4).

Numerous clusters of small sporangia are present in coal balls # 437A, 442, 679, and 680, from the Urbandale mine. Their compact aggregation in all cases suggests that these clusters represent small portions of highly compound fructifications comparable in complexity to those of *B. forensis* and *B. globosa* (fig. 3). It is apparent that each cluster consists of from 5 to 20 sporangia, terminating small frond ramifications. The attachment to these ultimate branchlets has only been noted in a few isolated cases, the branchlets themselves being very poorly preserved.

The individual sporangia are shortly pedicellate, and ovoid-ellipsoid in longitudinal section (fig. 1); in transverse section perfectly oval (fig. 2). The sporangia reach a maximum of .45 mm. in length and .25 mm. in diameter.

The sporangial walls are but a single cell thick. As seen in transverse section, the wall displays a differential thickening which served as an annulus. The largest cells of the annulus are approximately 50 $\times$ 50 μ in their transverse dimensions and about 75 μ in length. Their inner and radial walls are thicker than the free outer walls. The size of the cells decreases gradually, with the smallest cells measuring only 8–10 μ in thickness. Dehiscence occurred by means of a longitudinal cleft along the thinnest portion of the wall. The differential thickening of the sporangial wall may be clearly seen in figs. 1 and 2.

Numerous well-preserved spores are present in nearly every sporangium. They are of radial- trilete morphology (see fig. 4). The commissural, or inner surfaces, of the spores are compressed into three nearly equilateral triangular surfaces, each measuring about 36 μ along its basal side. The inner sides are delimited by a prominent triradiate ridge which extends nearly to the corners of the inner face. The spore walls are finely reticulate, the differential thickening producing extremely thin and translucent spots between the thickened ridges.

The small size of the sporangia and the distinctness of the spores warrant recognition of this fructification as a new species. The specific name *fecunda* is

proposed in reference to the prolificity with which the sporangia were produced.

Specific Diagnosis: Sporangia borne in compact terminal clusters of 5 to 20 each, pedicellate, ovoid-ellipsoid, reaching .45 mm. in length and .25 mm. in width. Largest cells of annulus averaging 50 × 50 μ in transverse dimensions. Spores radial, trilete, averaging 36 μ along the base of each triangular commissural surface, and with pronounced triradiate ridges; spore walls finely reticulate, with thin, translucent areolae.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1676–1680.

BOTRYOPTERIS **spinosa**, sp. nov. (figs. 5–8).

A single group of rather loosely aggregated sporangia with dimensions similar to those of *B. fecunda*, but of slightly different shape and with entirely distinct spores, was found in WCB 437B, from the Urbandale mine (fig. 6). The sporangia are much more loosely arranged than those of *B. fecunda*. The pedicellate attachment to a small ultimate rachis was clearly observed in one case (fig. 7). The sporangia average .50 mm. in length and .25 mm. in diameter. In longitudinal section they are somewhat narrowed at the base, resulting in a pyriform aspect. The sporangial walls are a single cell thick. The largest cells of the annulus measure approximately 50 × 50 μ in transverse dimensions and 70 μ in length (fig. 8).

The spores (fig. 5) are perfectly spherical, averaging 45 μ in diameter. A faint triradiate ridge is present, each leg not exceeding 10 μ in length. The spore walls are smooth, but distinct in being sparsely studded with blunt spines reaching 6 μ in length and averaging 2 μ in diameter. Calculations indicate a comparatively low spore output, not exceeding a hundred spores per sporangium.

This species is named *spinosa* with reference to the spinose ornamentation of the spore walls.

Specific Diagnosis: Sporangia borne in loosely aggregated clusters terminating the ultimate ramifications, shortly pedicellate, pyriform, averaging .50 mm. in length and .25 mm. in diameter. Largest cells of annulus averaging 50 × 50 μ in transverse dimensions. Spores spherical, trilete, averaging 45 μ in diameter, with faint triradiate ridges; spore walls sparsely provided with blunt spines reaching 6 μ in length and 2 μ in diameter.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1681–1683.

BOTRYOPTERIS **illinoensis**, sp. nov. (figs. 9, 10).

This description is based upon numerous isolated sporangia and one small cluster of eight, found in WCB 714 and 715, from Berryville, Illinois.

The sporangia are nearly spherical (fig. 10). The sporangial walls are a single cell thick, with the largest cells of the annulus measuring approximately 70 μ radially and 40 μ tangentially. No evidence of a sporangial pedicel has been observed.

The spores are quite distinctive (fig. 9). They are radial and trilete, with axial dimensions much smaller than the transverse. This is not due to crushing, however, as the spore walls are always fully distended. As seen in the transverse plane, the spores are roughly triangular, with rounded corners and markedly concave sides. The distance between corners averages 23 μ; the distance between one corner and the opposite concavity in the spore wall averaging 18 μ. The rounded tips average 10 μ in width. In axial dimensions the spores average 10 μ. The walls are thin, with a faint triradiate ridge, the legs of which extend approximately two-thirds of the distance to the tips of the lobes. Otherwise there are no distinct markings on the walls.

Although this fructification is entirely distinct from all other American fructification species of *Botryopteris*, it corresponds quite closely to those reported by Scott (1910) in association with the English species *B. antiqua*, *B. hirsuta*, and *B. ramosa*. However, the absence of these species in American coal balls and their greater geological age make it seem quite unlikely that the fructifications are conspecific with the Illinois specimens. Furthermore, the Berryville locality has produced to date two stem species of *Botryopteris*,[8] either of which may ultimately prove to have borne these sporangia. For this reason, in addition to the contrasting characters found between the Illinois specimens and all other American species, this fructification is recognized as an additional new species, the name *illinoensis* being proposed in recognition of its place of origin.

Specific Diagnosis: Sporangia ovoid, averaging .40 mm. in length and .30 mm. in diameter. Largest cells of the annulus averaging 70 $\times$ 40 μ in transverse dimensions. Spores radial, trilete, axially flattened, with rounded corners and concave sides, 10 μ in axial dimensions and 23 μ between corners; spore walls smooth, with faint triradiate ridges.

Age: McLeansboro Group of the Pennsylvanian.

Locality: Berryville, Illinois.

Type Slides: #1684–1686.

A comparison of the various species is presented in tabular form on the following page.

DISCUSSION

The sporangia discussed in the preceding pages, while belonging to an archaic fern genus, are striking in several respects. They have very delicate sporangial walls, a single cell thick. There is a differential thickening of the wall, suggestive of a primitive annulus. The sporangia themselves are very small, comparing closely with living osmundaceous sporangia in size. Finally, in at least the one species *Botryopteris spinosa*, spore output is relatively low, closely comparing to the Osmundaceae in this respect also.

While the coenopterid ferns have been variously known as the Primofilices (Arber, 1906), Coenopterideae (Seward, 1910), and Inversicatenales (P. Bertrand,

[8] In a recent communication, Dr. W. N. Stewart, of the University of Illinois, reported having found specimens of *B. radiata* Darrah in Berryville material. This locality is also the source of a yet unpublished new species of *Botryopteris*.

1909), they have invariably been considered as *eusporangiate* forms. As defined by Goebel (1880), one of the implications of this term is a sporangial jacket more than one cell thick. In this consideration alone the sporangia of *Botryopteris* fail to conform to the eusporangiates. While it is true that the bulky walls of sporangia of *Etapteris*, *Chorionopteris*, and *Stauropteris* allow no alternative but to consider the genera to be of eusporangiate nature, the thin-walled sporangia of *Botryopteris*, pointed out by Renault in his original description of the fructifications and by Scott and Bower, seem to offer grounds for doubting the validity of such an arbitrary scheme of classification.

COMPARISON OF THE VARIOUS FRUCTIFICATION SPECIES OF *BOTRYOPTERIS*

Species	Sporangial dimensions	Spore size	Spore morphology	Spore ornamentation
B. forensis Renault	1 × 2 mm.	70 μ	Spherical, trilete	Apparently smooth
B. americana Graham	1.30 × .70 mm. (?)	30 μ (?)	?	?
B. globosa Darrah	1.50 × 1 mm.	50–65 μ	Spherical, trilete	Smooth
B. sp. Scott	.28–.24 mm. diameter	25 μ	Triangularly flattened	?
B. fecunda Mamay	.45 × .25 mm.	36 μ along one side	Tetrahedrally compressed	Finely reticulate
B. spinosa Mamay	.50 × .25 mm.	45 μ	Spherical, trilete	With blunt spines
B. illinoensis Mamay	.40 × .30 mm.	23 μ between lobes	Axially flattened, triangular, with concave sides	Smooth

Hirmer (1927), although adhering rigidly to the eusporangiate concept of the coenopterids, has taken a forward step in introducing a scheme of fern classification in which the Osmundaceae are placed in a position intermediate between the Leptosporangiatae and Eusporangiatae, the subdivision to which they are assigned (Protoleptosporangiatae) enjoying equal rank with the Eu- and Leptosporangiatae. The genus *Botryopteris* cannot be conclusively assigned to either of these two main groups, in view of the admixture of both primitive and advanced characters. It is highly probable that as our knowledge of the fossil ferns advances, the coenopterids eventually will be considered to be less closely interrelated than they have been previously, and that the great structural differences to be found among their fructifications will gain recognition in a revised classification.

Marattiales

This order, embracing a single family with seven living genera and a large complex of extinct forms, is characterized by its eusporangiate, exannulate fructifications consisting of more or less synangial, clearly circumscribed sori which are borne superficially.

The majority of the Carboniferous Marattiaceae bore radially symmetrical sori, and as has been pointed out previously by Hoskins (1926) and Graham (1934), these fructification genera were placed by Stur (1883) in a suborder of the Marattiales, the Asterotheceae. This suborder includes only fossil forms, now totaling six genera, two of which (*Scolecopteris* Zenker and *Cyathotrachus* Watson) have been found to occur rather abundantly in the American coal balls investigated in this study. In addition to these two genera, whose histories are reviewed in succeeding pages, the Asterotheceae include the following:

Acitheca Schimper: Synangia sessile; sporangia attached at their bases to a central column, with distal portions free; sporangial apices long and bristle-like. (For historical details see discussion of *Scolecopteris*.)

Asterotheca Presl: Synangia sessile; sporangia attached to a central receptacle, but free distally, their long axes parallel to the plane of the pinnule. Genus founded by Presl (Corda, 1845), and originally considered to be gleicheniaceous by Corda. Several species known, chiefly from compression material.

Ptychocarpus Weiss: Synangia pedicellate; sporangia enclosed in a continuous synangial sheath, and fused to a central column extending through the entire length of the synangium. Genus founded in 1869; the best-known description is that of *P. unita* Brongniart, by Renault (1896). (See fig. 11.)

Sturiella Weiss: Synangia pedicellate; sporangia basally fused but free above, each sporangium with an apical annulus-like structure. Genus founded by Weiss (Zeiller, 1890); a detailed description presented by Renault (1883) as *Pecopteris intermedia*. The presence of the annulus-like structure, along with the synangial nature of the fructification, has caused *Sturiella* to be regarded as intermediate between the Marattiaceae and Osmundaceae.

These genera are limited mainly to strata of Upper Carboniferous age, and are all known to exist in organic connection or intimate association with foliage of the *Pecopteris* type.

Although many of the petrifications investigated in this study contain an abundance of fructifications belonging to several genera, *Asterotheca* and *Ptychocarpus* are totally lacking. While petrified specimens of these two genera have been reported in the literature, they are represented in large part by compresséd specimens. This situation suggests a problem in preservation phenomena.

It has been pointed out by Kidston (1925) and Arnold (1947) that the single major difference between *Scolecopteris* and *Asterotheca* lies in the fact that the former is pedicellate, the latter sessile. In all other features, such as size and shape of the sporangia and manner of dehiscence, they are essentially alike. Studies of petrified *Scolecopteris* specimens have shown that with maturity the sporangia be-

came radially extended from each other, much as the ribs of an opening umbrella; in this condition they closely approach the typical aspect of *Asterotheca*, discounting their pedicellate nature. If sufficiently extended prior to compression, the fructifications would eventually be preserved with the sporangia arranged in a typical asterothecoid fashion, with the pedicel totally obscured from view. There would thus be no dependable method of determining the true generic affinity of the specimen. Although it is not my intent to question the validity of the genus *Asterotheca*, the following pertinent facts should be given careful consideration:

1. Petrified fructifications referable to *Asterotheca* have not been recognized during this study,[9] while *Scolecopteris* has been found in great abundance.

2. While the vast majority of accounts dealing with *Asterotheca* have been based on compression material, the exact reverse holds true for *Scolecopteris*.

Due to the reasons presented above it would appear that positive identification of compressed fructifications must not be made without careful consideration of the possibilities for generic confusion. A similar situation might exist in the genera *Ptychocarpus* and *Cyathotrachus*, which differ only in the extent of the central column, a feature which does not readily lend itself to accurate determination in the compressed form. While *Ptychocarpus* is found prolifically as compressions, in only two instances has it been reported in the petrified state in American literature.[10] On the other hand, while three species of *Cyathotrachus* are known from petrifactions, not a single compressed specimen has ever been reported, all compressed fructifications in which the sporangia are surrounded by a continuous synangial sheath being referred to *Ptychocarpus*.

CYATHOTRACHUS Watson, emend. Mamay.

C. ALTUS Watson, Roy. Micr. Soc. Jour. 1906. 1–3.

C. BULBACEUS Graham, Bot. Gaz. 95:459–461. 1934.

The genus *Cyathotrachus* is the most recent addition to Stur's (1883) Asterotheceae. Although the publication in which the genus was established appeared several years later than that of Stur, Graham (1934) was the first to recognize the asterotheceous affinity of the fructification and point out the necessity for including it within that group.

Watson's type species, *C. altus*, is from the Lower Coal Measures of England. His discovery of a cup-like tracheidal structure in the base of the synangium led to the adoption of the generic name *Cyathotrachus*. The specific name *altus* refers to the height of the fructification. Although his description does not include a clear statement of the generic characters, he apparently considered the tracheidal cup to be of primary importance. This concept has, however, been altered by subsequent discoveries. Graham, in describing the second species, *C. bulbaceus*, from the Upper Pennsylvanian of Illinois, failed to recognize any such structure

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[9] Benninghoff (1943) briefly mentioned the presence of *Asterotheca* in Indiana coal balls.

[10] *Ptychocarpus* has been reported by Benninghoff (1943) and Hoskins (1933).

in his specimens and considered that its presence or absence could possibly constitute a generic difference. I have studied several scores of specimens from Iowa coal balls, paying particular attention to this detail, and I did not observe the tracheidal cup in a single fructification. Notwithstanding, there is ample evidence to support the belief that the two above-mentioned species and a third, described below, are congeneric. It appears that the fructification was inaptly named, since the generic name refers to an inconstant character which should be considered to be of only specific importance. The character of prime generic importance would seem to be the cup-like arrangement of the fructification itself.

An emended concept of the genus is presented in the following diagnosis:

Generic Diagnosis: Synangia pedicellate, circular, containing several more or less elongate, exannulate sporangia, the entire fructification enclosed in a continuous outer synangial sheath, with the exception of the apical pore. Basal portion of the synangium with a central column; apical portion hollow and cup-like.

CYATHOTRACHUS **altissimus**, sp. nov. (figs. 12–16).

The description is based upon numerous specimens scattered through several of the Urbandale coal ball slabs from the Thompson collection. Although usually occurring singly, a few specimens consisting of several closely associated synangia were found. In several instances it was possible to select specimens for further study with the naked eye, because of the large size of the fructifications and the characteristic bright golden color of their spore masses, which were in striking contrast with the less conspicuously colored matrix.

Although the number of sporangia in a synangium ranges from 5 to 9, those with 7 are predominant. The innermost walls of the sporangia are fused with the tissue of a central column[11] that extends slightly beyond the middle of the synangium. The column flares out somewhat at the distal end, forming a shallow saucer-like structure beyond which the synangium is hollow and resembles a deep cup. Proximally, the column extends beyond the bases of the sporangia to form the short synangial pedicel. The column is composed of elongate thin-walled cells averaging approximately 25 μ in diameter and 300 μ in length. There is no evidence of vascular elements in this structure.[12] Average dimensions of the central column are approximately .20 by .80 mm. (fig. 12).

Individual sporangia average 1.50–1.80 mm. in length and .20–.45 mm. in diameter, the radial dimensions being slightly greater than the tangential, due to lateral appression with adjacent sporangia. The synangia as a whole average .80–.90 mm. in diameter. Throughout the portion of the synangium that is traversed by the central column, the lateral walls of the sporangia are so closely appressed as to present the appearance of a single wall (fig. 15), but progressing distally beyond the termination of the column the walls of adjacent sporangia can

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[11] Watson (1906) termed this structure a "columella", but this usage is questionable, since the column is not, in this case, a structural entity of the sporangium proper.

[12] Watson (1906) found tracheids in this column, and Graham (1934) termed this tissue "transfusion tissue" without further elaboration.

be distinguished from each other. The character of the sporangial walls is best seen in dehiscent synangia (fig. 16). The cells are thin-walled, and there appears to be only one layer. The outer surface of the synangium is enclosed by a continuous layer of thin-walled cells corresponding very closely to the synangial wall found in *Ptychocarpus*. This layer of tissue partially fills the angles created where the lateral walls of adjacent sporangia depart from each other, and varies from one to three or four cells in thickness. Serial sections indicate that the synangial wall increases in thickness as the distal end of the synangium is approached. This structure is shown in fig. 13. The fact that it is not present in all specimens indicates that it may have been rather fragile tissue, probably drying at maturity and being either blown off by the wind or rubbed off by friction with adjacent synangia.

The cellular details of the pinnules were observed in a few isolated fragments. The upper epidermis is highly cuticularized and shows no cellular detail, being seen only as a dense black line. Beneath the palisade layer the cells are rather loosely aggregated and show no apparent differentiation, with the exception of the one or two lowermost layers of cells, which are flattened in the plane of the lamina surface. These appear to be a continuation of the pedicel, showing a close similarity to its tissue both in size and shape of cells. The pedicel is very short and thick, and the tissues composing it are not distinguishable from those of the central column. The manner in which the synangia were oriented upon the surface of the lamina was observed in one specimen. This consists of several distinct rows of compactly arranged synangia oriented at right angles to a structure which appears to be the midrib of a penultimate pinnule, two adjacent rows of synangia probably representing the fructifications produced by a single ultimate pinnule. Unfortunately, that portion of the coal ball containing the remainder of the specimen was not among the slabs presented by Mr. Thompson, and we have not been able to ascertain the relationship between the rows of synangia and the parent pinnules, or the nature of the pinnules. Since the two previous species are known to be in close association with *Pecopteris* foliage, and since the orientation of the synangia in this specimen seems to correspond closely with that of other asterotheceous pecopterid fructifications, it seems safe to assume that this species was borne on foliage of the *Pecopteris* type.

Neither Watson nor Graham described the dehiscence of *Cyathotrachus*, but fortunately many of the Iowa specimens illustrate that feature very well. Dehiscence was accomplished by means of longitudinal slits along the inner walls of the sporangia, extending from the sporangial apices as far as the proximal limits of the hollow portion of the synangium. Although no specialized stomial or annulate structures were present, the inner surfaces of the sporangia, being the thinnest, offered the line of least resistance, with the results described here. Dehiscence of the sporangia was accomplished by a rupturing of the outer envelope of the synangium and separation of the closely appressed walls of adjacent sporangia; this release of both lateral and peripheral tension allowed the sporangia to

assume a more nearly cylindrical appearance than that displayed prior to dehiscence. That portion of the sporangium adjacent to the central column, however, was not altered by dehiscence; lateral walls remained closely appressed with those of the adjacent sporangia, and the synangial wall remained intact. Figure 15 shows a transverse section of a sporangium that has already shed its spores. Here the section has been taken through the central column, and the synangial wall is still a continuous tissue surrounding the entire structure. Dehiscence is further illustrated in fig. 16, in which the spores are being shed into the hollow synangial cup.

Spores of this species are small, with bilateral-monolete symmetry, averaging 12 × 20 μ in dimensions. The walls are smooth, with the exception of a single faint longitudinal suture that is seen on the concave side of better-preserved spores. Judging from the relative dimensions of the spores and sporangial cavities, it appears that several thousands of spores were produced in each sporangium. Figures 13 and 14 illustrate the bean-like shape of the spores and the abundance in which they were produced. Tetrads have not been observed.

Cyathotrachus altissimus differs in several ways from the two previously described species. In general proportions it corresponds rather closely with the type species, *C. altus*, but differs sufficiently in size, number of sporangia, and spore characters to warrant recognition as a separate species; likewise the differences from *C. bulbaceus* are equally significant. The more important characters of the three species are presented in the following table:

	C. altus Watson	*C. bulbaceus* Graham	*C. altissimus* Mamay
Sporangial dimensions	.20 × .70 mm.	.30–.35 × .65 mm.	.20–.45 × 1.50–1.80 mm.
Number of sporangia per synangium	4–7	4–6	5–9
Spores	Ovoid, 12.5 × 15 μ	Round, 18 μ in diameter	Bilateral, 12 × 20 μ

In reference to the proportionately greater height of the synangium than that of the type species, the specific name *altissimus* is proposed and the following diagnosis offered:

Specific Diagnosis: Synangia containing 5–9 sporangia; central column extending approximately half the length of the synangium. Sporangia 1.50–1.80 by .20–.45 mm. Dehiscence by a longitudinal cleft along the innermost sporangial wall. Spores monolete, bilateral, measuring approximately 12 × 20 μ; spore walls smooth, with a single longitudinal suture along the concave surface.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1687–1693.

DISCUSSION

The genus *Cyathotrachus* was considered remarkable by its discoverer from the standpoint of its striking similarity to the fructification of the living marattiaceous genus *Christensenia.* This similarity has been pointed out by other authors; the chief difference between the two fructifications lies in the mode of dehiscence, which occurs by means of apical pores in the latter. Notwithstanding its gross similarity to the living genus, Watson was reluctant to assign conclusively his discovery to the Marattiaceae for the reason which he thus expressed:

> I think that two years ago no one would have hesitated to say that it belonged to the Marattiaceae. Now, however, in view of Mr. Kidston's discovery that *Crossotheca,* formerly considered to be Marattiaceous, is really the male fructification of *Lyginodendron,* whose female fructification is, of course, the seed *Lagenostoma,* it seems safer to regard it as of uncertain position, although belonging to either the Ferns or Cycadofilices, and I think most probably to the Ferns. For this reason I have put the word "Fern" in inverted commas in the title.

Although specimens referable to this genus have not been found in numbers sufficient to attract much attention,[13] other authors (Hirmer, 1927; Scott, 1920; Seward, 1910; Arnold, 1947) have remarked on its close similarity to the genus *Ptychocarpus.* The similarity may be noted by a comparison of figs. 11 and 13, the former being a reproduction of Renault's original illustration of *P. unitus* Brongniart. If the central column were removed from the latter, the two fructifications would indeed be morphologically identical; furthermore, discounting the presence of a vascular strand in the central column and the fact that the spores are still contained within the sporangia, Renault's figure might find a favorable comparison with the specimen shown in fig. 15. As a pertinent opinion, we quote Scott (1920), who wrote: "The fructification of *Ptychocarpus unitus* is, however, a good example of a typical Marattiaceous synangium, and affords strong evidence as to the affinities of the plant."

Considering the undeniable morphological similarities between the two genera, it seems that the opinion expressed above should apply to *Cyathotrachus* as well as *Ptychocarpus.* Indeed, it appears that the bulk of the evidence weighs in favor of a marattiaceous affinity for *Cyathotrachus.* Further pertinent discussion will be presented in succeeding pages.

SCOLECOPTERIS Zenker, Linnaea 11:509–512. 1837.

This fructification genus was based upon silicified material from the Lower Permian of Saxony, the type species being S. *elegans.* Although the scope of Zenker's original descriptions was somewhat hampered by the poor quality of preparations available to workers of his time, the generic diagnosis is sufficiently complete that confusion of this fructification with other genera is not likely. The original diagnosis is as follows: "Capsulae hypophyllae non zonatae binae—quinae

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[13] The only other specimens reported appeared in Darrah's (1941) treatment of the American coenopterid ferns, in which he reported "sporangia which have *Cyathotrachus* structure."

in unum glomus breviter stipitatum aggregatae, apice longitudinaliter hiantes. Indusium nullum."

The generic name literally means "worm fern" (Greek σκώληξ, worm; πτερίς, fern). The name was proposed in reference to the superficial resemblance of the numerous crowded pinnules to the segmented bodies of a host of maggots! This superficial similarity later caused Geinitz (1872) actually to interpret silicified *Scolecopteris* specimens as fossil millipedes; he named his specimens *Palaeojulus dyadicus* on this account (*Julus* being a modern millipede genus). Subsequent searches for the heads of these "worms" demonstrated the presence of attached fructifications and the errors of his interpretations.

In 1874 Strasburger made a more detailed investigation of Zenker's original material and redescribed the fructifications in a work which has since won acclaim among paleobotanists. This paper includes a critical comparison of the fructifications with those of other ferns and indicates his acceptance of the marattiaceous affinity of *Scolecopteris*.

Grand'Eury (1877) published very brief accounts of two additional species, S. *subelegans* and S. *ripageriensis*, from the Carboniferous of France. Although he attributed an "indusial" structure to S. *subelegans*, its presence is by no means clearly indicated. Furthermore, the two illustrations, which appear in natural size and a magnification of only two diameters, respectively, hardly present a basis for satisfactory comparisons of these fructifications with other species of *Scolecopteris*.

Several years later Renault (1883) described the fructifications of *Pecopteris polymorpha* under the name *Scolecopteris polymorpha*. His well-known drawing of this species, which appears in almost every text-book of paleobotany, shows the synangia arranged in a single series on either side of the pinnule midrib. They are sessile, and are composed of four sporangia each, fused at their inner surfaces to a central column which extends about a third of the distance from the base. The sporangia have long, bristle-like apices. In spite of the sessile attachment of the fructifications and the central column, Renault considered it to be within the generic limits of *Scolecopteris*. This point met with disagreement in 1890 when Schimper removed the fructification genus from *Scolecopteris* and created the new genus *Acitheca* in recognition of the generic significance of the difference between sessile and stalked synangia. Kidston (1925) concurred with Schimper's views.

Scolecopteris was assigned to the suborder Asterotheceae of the Marattiales by Stur, in 1883. The suborder was segregated to include fructifications in which the sporangia are stellately arranged; its original inclusions were the genera *Scolecopteris* Zenker, *Diplazites* Goeppert (*Ptychocarpus* Weiss), *Sturiella* Weiss (*Renaultia* Stur), and *Asterotheca* Presl. The asterothecous affinities of the two additional genera, *Acitheca* Schimper and *Cyathotrachus* Watson, which were not known at the time of Stur's publication, were pointed out by Graham (1934).

The first American addition to the genus *Scolecopteris* was made in 1926 when Hoskins recognized a new species, S. *minor*, from the Pennsylvanian of Illinois.

As evident from the specific name, this species is distinctive in its relatively small size.

In 1932 Scott described an additional species, *S. Oliveri,* based upon silicified specimens from the Permo-Carboniferous of Autun, France. This was followed in 1933 by a paper in collaboration with Holden, in which the foliage of the species was described. The silicifications are apparently the acme of preservation, and the descriptions and illustrations are correspondingly gratifying. The species is quite distinct from others, chiefly in its bilateral spores and the dimensions of the fructifications. Of exceptional interest, however, is the fact that the material was so well preserved that minute studies of such intimate details as epidermal hairs, ramenta, hydathodes, and stomata were possible.

Graham (1934) described the second American species, *S. latifolia,* from the Upper Pennsylvanian of Illinois. This fructification is distinct from ones previously described in its much larger spores (at least twice the diameter of other species known at the time of his publication) and the extremely inflexed, broad margins of the pinnules, from which the specific name was derived. In the same publication he reported specimens which he considered to belong to *S. minor* Hoskins, in spite of noticeably smaller pinnules and other differences, which he attributed to environment.

Andrews (1943) described the species *S. Radforthii* upon the basis of compressions from the McLeansboro formation in Illinois. Although the spores correspond closely in size with those of *S. latifolia* Graham, sporangial dimensions are not in close agreement, and the foliage shows no indication of the broad revolute nature of the latter species.

Following is a list in chronological sequence of the species known prior to this study.

S. *elegans* Zenker, Linnaea 11:509. 1837.
S. *subelegans* Grand'Eury, Acad. Sci. Inst. France, Mem. 24:72–73. 1877.
S. *ripageriensis* Grand'Eury, *Ibid.* 73.
S. *minor* Hoskins, Bot. Gaz. 82:427–436. 1926.
S. *Oliveri* Scott, Linn. Soc. [London] Jour. Bot. 49:1–12. 1932; *Ibid.* 309–321. 1933.
S. *latifolia* Graham, Bot. Gaz. 95:456–458. 1934.
S. *Radforthii* Andrews, Mo. Bot. Gard. Ann. 30:435–437. 1943.

During the past three years, many specimens of *Scolecopteris* fructifications have been studied, with the result that three new species and a tentative new variety are recognized. Furthermore, significant data have been added to our knowledge of *S. latifolia* Graham. The descriptions of this material are presented in the following pages, and at the conclusion of this chapter appears a chart comparing the significant characters of the various species, as far as they are known.

SCOLECOPTERIS LATIFOLIA Graham, emend. Mamay (figs. 17–23).

Numerous fructifications which are thought to be referable to *S. latifolia* have been observed in coal balls from various of the Iowa localities (chiefly Urbandale).

Faulty preservation and lack of associated foliar remains, however, render a positive identification of the fructifications impossible.

In recently collected coal balls from the Mineral, Kansas, locality it has been my good fortune to discover comparatively well-preserved fructifications, complete with foliage, whose identity as *S. latifolia* can hardly be questioned. However, in spite of the close correlation between various characters of our material and those given in Graham's descriptions and illustrations (1934), the Kansas specimens present significant differences which require careful consideration and warrant an emendation of Graham's original specific diagnosis.

The synangia predominantly contain three sporangia, but groups of four are comparatively common, while none with more than four have yet been found (fig. 18). The sporangia are attached at their bases to a common pedicel (fig. 17). No evidence of vascularization of the pedicel has been observed. Above the point of attachment with the pedicel the sporangia of a single synangium are quite free from each other, although in some instances they are so closely appressed that an illusion of a connection is created. There is no central column in the synangium as indicated by Graham.

Individual sporangia vary from .90 mm. to 1.20 mm. in length and from .39 to .34 mm. in width; the width is usually greatest near the base and decreases gradually toward the distal end, resulting in an acute sporangial apex (fig. 17). The outer, or free surfaces, of the sporangial walls are not appreciably thicker than the inner. When seen in transverse sections (fig. 18), the sporangia are roughly triangular, due to the close appression with adjacent ones. Dehiscence occurs, as in all other species of *Scolecopteris*, by means of a longitudinal cleft along the innermost surfaces of the sporangia.

The spore contents of the Kansas material leave much to be desired from the standpoint of preservation. Although the majority of the sporangia are nearly filled with spores, the spores are mostly collapsed or fragmentary and were apparently preserved prior to maturity, judging from the great variability in their sizes. The spores are trilete, the better preserved ones up to 35 μ in diameter. The spore walls are without any distinctive sculpturing, but faint triradiate markings have been seen in a few specimens (fig. 20).

The pinnules are arranged alternately upon the penultimate midrib, and when seen in sections transverse to the midrib have margins which are so inflexed that they nearly form a closed chamber or cylinder (fig. 17). Measured at the "shoulders," the pinnules average 2 mm. in width. This does not, however, embrace the entire width, for if the inflexed margins were flattened out the width would then approach 7 mm. Figure 17 illustrates this aspect of the pinnules very well. Here are shown two pinnules, each bearing two fructifications which are nearly enclosed by the foliar margins. The short pedicel may be seen attaching one of the synangia to the pinnule at the right. The upper surface of the pinnule is composed of an epidermal layer with a relatively thick hypodermis, the two being indistinguishable from each other. The cells of this region are filled with a dense

black substance. The lower epidermis is a very thin layer, probably a single cell thick. Between the upper epidermis and the lower the tissues are not preserved. The midrib is relatively small, and the vascular tissue is not preserved. (The midrib of the penultimate pinnule, however, has been seen to contain a u-shaped vascular strand with the open ends oriented adaxially.) Slightly below the "shoulders" of the pinnule the dense tissues of the upper and lower surfaces merge into a single tissue which composes one-third of either side of the lamina.

As seen when sectioned in the plane parallel to the lamina proper, the pinnules average 3.80 mm. in length and display the typical pecopterid outline (figs. 19 and 23). In fig. 23, the section has intercepted several of the unbranched lateral veins. The several synangia, which are sectioned very near their proximal ends, are seen to be inserted directly below the lateral veins in a single series on either sidé of the midrib. Figure 18, showing a specimen sectioned in a plane somewhat lower than that in fig. 23, illustrates the epidermis and hypodermis with their dense contents. Here we see eleven fructifications sectioned transversely; of these, seven contain only three sporangia each. Proceeding further downward in this series, it soon becomes apparent that we are dealing with a type of pinnule which is unique for the genus *Scolecopteris*. As the upper and lower epidermal layers merge to form the single homogeneous tissue described above and illustrated in fig. 17, this tissue becomes dissected, resulting in an *incised margin* to the pinnule. This is illustrated in fig. 19. Here the essentially pecopterid outline of the pinnule is preserved, but the margin is seen to be composed of not a continuous line of tissue, but of a series of small crescent-shaped segments averaging .50 mm. in length and .15 mm. in width, with the convex surfaces directed toward the midrib of the pinnule. In this figure, the outline of one pinnule is seen extending away from the rachis, with segments of the margins of two adjacent pinnules also present. The discreteness of the marginal lobes is best shown in fig. 21. The lamina proper, with fragments of several longitudinally sectioned fructifications attached, is seen in the upper portion of the illustration. At the lower portion appear the several marginal lobes of the pinnule. They are well-defined, separate bodies with dense cellular contents corresponding exactly to those seen in figs. 17, 18, and 19. Another conspicuous feature are the multicellular hairs attaining lengths of .50 mm., which arise from both the dorsal and ventral surfaces of the marginal lobes. Figure 22, showing a single enlarged lobe (sectioned transversely), illustrates especially well the dense cellular contents and the multicellular hairs.

By serial sections of the Kansas specimens, the following facts pertinent to *S. latifolia* have been established:

1. The lateral veins of the pinnule extend only approximately as far as the "shoulders" of the pinnule. Beyond this point they are indistinguishable, and beginning at approximately the point where they disappear, the lamina becomes dissected, the number of resultant marginal lobes usually corresponding to the number of veins. The margins of the lobes fall in the area between the veins.

2. The fructifications are inserted singly, below and near the ends of the veins; they are accordingly situated very close to the bases of the marginal lobes.

From the above information inferences of phylogenetic interest may be made which will be taken up in detail later in this paper.

In several respects the Kansas specimens correspond sufficiently with the type description that their identity with *S. latifolia* is obvious. They concur exactly in the dimensions of the fructifications, numbers of sporangia in the synangia, and in the shape and total width of the pinnules, as seen in transverse sections. A completely satisfactory comparison of the spores is not possible, but they are alike in having triradiate markings and smooth exines. Furthermore, the measurements of the spores of our material agree with Graham's specifications.

Graham described a central column in the synangium. This I attribute to a misinterpretation on his part. Such a structure, although shown in his line drawing (fig. 7 of his paper), is not apparent in the photograph which appears in his figure 27, or in his original slides.[14] In his illustration and the Kansas specimens the closely appressed walls of adjacent sporangia superficially seem to be fused organically. Minute examination of the Kansas specimens has invariably proved that this is not the case, however. If a central column were present, the fructification would indeed be beyond the limits of *Scolecopteris* and would represent a fructification intermediate between the genera *Scolecopteris* and *Acitheca*.

The dissected margin of the pinnule was not mentioned by Graham. This feature is not clearly seen in Graham's slides due to inferior preservation and absence of a section comparable to that shown in fig. 19. While it is not my intent to confuse the nomenclature of the genus, it seems that the results of this study necessitate an emendation of Graham's concept of *S. latifolia*, with particular reference to the central column and the margination of the pinnules.

Emended Specific Diagnosis: Synangia consisting of usually 3, sometimes 4, sporangia. Sporangia with acute apices and ranging from .90 to 1.2 mm. in length and from .34 to .39 mm. in width, attached basally to a short synangial pedicel, but free above; outer surfaces of walls not appreciably thicker than the inner; dehiscence by means of a longitudinal cleft along the innermost sporangial wall. Pinnules averaging 3.80 mm. in length and with total widths averaging 6.50 mm., strongly inflexed and deeply incised on the margins, with a single synangium inserted near the base of each marginal lobe and directly beneath a lateral vein; lobes averaging .50 mm. in width, with multicellular hairs borne on both surfaces. Spores spherical, to 35 μ in diameter, with trilete scars and otherwise smooth exines.

Age: Fleming coal, Cherokee shale.

Locality: Mineral, Kansas.

Type Slides: #1694–1697.

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[14] Graham's type slides of *S. latifolia* were made available for this study through the kindness of Dr. R. M. Kosanke, of the Illinois State Geological Survey.

SCOLECOPTERIS **iowensis**, sp. nov. (figs. 24–28).

Several small Urbandale coal ball slabs (WCB 511, 515, 517, 518) were found to contain an abundance of these fructifications, in many cases attached to the pinnules. The color and texture of the slabs WCB 511, 515, and 517 indicate that they probably were cut from the same coal ball, but this cannot be verified since they were sent to this laboratory already sawed.

The synangia consist of four, five, or most commonly six, elongate sporangia. They are arranged circularly and are attached at their bases to a common pedicel. The fructifications are inserted in a single or sometimes double series on each side of the pinnule midrib. The synangia average about 1 mm. in length (including the pedicel), and about .90 mm. in diameter, this dimension being dependent upon the extent to which the sporangia have spread radially. The individual sporangia average about .90 mm. in length and .33 mm. in width, with the greatest diameter usually being very near the base. Although attached at their bases to a common pedicel, the sporangia are separated throughout their entire lengths. In longitudinal section (fig. 27), they are seen to taper toward their distal ends, terminating in bluntly acute apices. The sporangial cavity, however, is roughly ovoid in longitudinal section, the sporangial apex being formed by the elongate wall cells and not representing a continuation of the cavity. The cells of the sporangial walls are approximately 30 μ in diameter and 150 μ in length.

Although preservation of the cells is not altogether complete, a sharp contrast may be noted between the outer and lateral walls of the sporangium (fig. 26). The outer walls are thicker, consisting of two or three layers of cells which have thickened walls and usually contain a dense black substance; the lateral walls, on the other hand, contain only one layer of cells which lack these thickened walls and black contents. In all the specimens examined, the cells of the lateral sporangial walls are lacking the cell wall on the side facing the adjacent sporangium (fig. 26). This condition, together with the fact that the sporangia appear to be laterally flattened in transverse section, suggests that the sporangia were probably very closely appressed prior to maturity; the separation of the sporangia upon reaching maturity very likely ruptured the walls of these cells, explaining their absence in our specimens.

Dehiscence was accomplished by means of a longitudinal slit along the innermost surface of the sporangial wall (fig. 28). The majority of the sporangia shown in this section exhibit dehiscence slits and have shed their spores.

The pedicels average about .15 mm. in length and .20 mm. in width. Their component cells are of thin-walled parenchymatous nature, measuring about 30 μ in diameter and 45 μ in length (fig. 27). There is no evidence of vascularization of the pedicel.

The spores constitute the most distinctive single feature of this fructification. In size they exceed those of all other species of *Scolecopteris*, attaining diameters of 80 μ, but averaging about 65 μ. Distinct triradiate markings and delicate reticula-

tions of the exine are present (fig. 25). The spore output was relatively small, probably not exceeding 100 per sporangium.

The pinnules have strongly inflexed margins. Normally they average about 3.50 mm. in width and 7 mm. in length, but if the inflexed margins were to be flattened out the width would be increased to about 5 mm. The structure of the pinnule is fairly well known. Figure 24 shows it to possess a strong midvein containing a terete vascular strand surrounded by large thin-walled cells, probably parenchymatous. A well-developed palisade layer is present. The upper epidermis is heavily cuticularized; the lower epidermis is also, but to a lesser extent. The mesophyll tissue lying between the point of insertion of the synangia and the margin of the pinnule consists of flat plate-like cells whose greater axes parallel the plane of the pinnule surface.

The specimen represented in fig. 24 indicates that the synangia were ordinarily borne in a single series on each side of the midvein. However, instances of departure from that condition have also been noted. Figure 28 shows a section taken through the midvein of a pinnule in a plane parallel to the plane of the lamina. Here is shown a lateral vein departing from the midrib, with two distinct rows of synangia lying parallel to the midvein. These two rows of synangia might be interpreted as belonging to two separate adjacent pinnules, but thorough investigation of this and other comparable specimens reveals that the synangia of one row are much too closely appressed with those of the other to accommodate the two inflexed pinnule margins which otherwise would have occupied the position between rows. This would indicate, then, that a single series of synangia on each side of the midvein was not always the case, some of the pinnules apparently having borne two rows of fructifications on each side.

In consideration of the spores alone, this fructification appears to be a distinct species of *Scolecopteris*. Spores of this species are seen to reach diameters of 80 μ, while those of all other species are much smaller, with the exception of S. *latifolia* and S. *major* (description on following pages). In S. *latifolia* they are known to attain a maximum diameter of 35 μ; furthermore, the predominance of trilocular synangia, the sporangial dimensions, and unthickened outer sporangial walls of S. *latifolia* are in striking contrast to the usually 6-locular synangia, smaller sporangia and unequally thickened sporangial walls of S. *iowensis*. The specific distinctions between S. *iowensis* and S. *major* (discussed below) leave no alternative but to recognize this fructification as a new species. The name S. *iowensis* is proposed with reference to the type locality, and the specific characters are summarized in the following diagnosis:

Specific Diagnosis: Synangia borne in single or double series on each side of midvein and consisting of 4, 5, or, most commonly 6, sporangia. Sporangia free laterally, attached basally to a common pedicel, averaging approximately .35 mm. by .90 mm.; outer surfaces of walls thickened, inner surfaces thin; dehiscence by a longitudinal cleft along the innermost surface of the sporangial wall. Spores round, 65–80 μ in diameter, with triradiate scars and reticulate exines. Pinnules

averaging 7 mm. in length, normally about 3.5 mm. wide, but 5 mm. wide if unrolled.

Age: Des Moines Series of the Pennsylvanian.
Locality: Urbandale Mine, Iowa.
Type Slides: #1698–1702.

SCOLECOPTERIS MINOR Hoskins, var. **parvifolia**, var. nov. (figs. 29–33).

This extremely small fructification with its proportionately small supporting pinnules has proven to be the most abundant and widely distributed form of *Scolecopteris*. Its presence was first noted in coal balls 431 and 445, from the Urbandale Mine in Iowa, and it is chiefly on this material that the following description is based. Since the beginning of this study, however, petrifactions from several other localities have been collected and sawed, and fructifications which correspond exactly with the original material have been found in coal balls from Lynnville, Ind., Berryville, Ill., Mineral, Kans., and in one tiny fragment from Shore, Lancashire, England.

An outstanding specimen consisting of the greater portion of an ultimate rachis and several attached pinnules was found in WCB 431. Although the original saw-cut sectioned the specimen slightly obliquely to the plane of the lamina, it clearly illustrates the nature of the pinnules and their fructifications.

The synangia usually contain only four sporangia, but groups of five are not uncommon and one synangium with six was found. The synangia average about .70 mm. in diameter and .65 mm. in length, including the pedicel. They are always arranged in a single series on each side of the midvein, on the dorsal surface of the pinnule. The individual sporangia are ovoid in longitudinal section, averaging from .56 to .60 mm. in length and about .35 mm. in diameter. In longitudinal section (fig. 33) the sporangial apices are seen to be more blunt than those of S. *iowensis*. Here again, the apex is formed by elongate wall cells and does not represent a continuation of the sporangial cavity. The sporangia are grouped about the common pedicel, which in this species superficially resembles a very short central column, due to the slightly oblique basal attachment of the sporangia. Basally the sporangia are closely appressed to each other (not organically fused, however); for the greater part of their lengths the lateral walls are entirely free from each other.

The outer sporangial walls are thickened, usually entailing two or more layers of cells with very heavy walls. The inner walls contain only a single layer of cells whose walls are not thickened as those of the outer wall cells. Dehiscence was accomplished by means of a longitudinal cleft along the innermost surface of the sporangial wall. The transverse aspect of dehiscent sporangia is shown in fig. 31.

The pinnules of this species are much smaller than those of other species. They seldom exceed 4 mm. in length, averaging about 3 mm.; width averages about 1.75 mm. The margins are strongly inflexed, however, and if they were flattened out the width would be increased to about 2.50 mm. The nature of the pinnules is

shown in fig. 32. This section has been cut through the lamina on one side of the midrib and through the attached synangia on the other side. The strong ultimate rachis may be seen with the pinnule midvein departing from it. Lateral veins are seen departing from the pinnule midvein. There are five synangia and five lateral veins in evidence, their relative positions indicating that the fructifications are borne directly beneath the veinlets. There is no evidence of incision of the margins. Figure 29 is a transverse section of a pinnule, further illustrating the strongly inflexed condition of the margins. Also shown is a strong midvein, although faulty preservation precludes a detailed study of the vascular tissue. Palisade tissue seems to be lacking, and the epidermal layers show no apparent cuticularization. The uniseriate insertion of the fructifications is shown in fig. 32.

The spores are badly crushed in the majority of the specimens. There is, however, a triradiate scar present, although the exine is without any additional markings. The spores are spherical, averaging approximately 15 μ in diameter (fig. 30).

Spore and sporangial dimensions distinguish this fructification from S. *latifolia*, S. *major*, S. *elegans*, and S. *iowensis*, while the morphology of the spores serves in itself to separate it from S. *incisifolia* (description to follow) and S. *Oliveri*. Had this study been limited to inspections of only a few specimens, they might have been referred to S. *minor* because of the strong resemblance. However, in view of the constancy of the cited dimensions in numerous specimens from several widely separated localities in America and one in England, the smaller sporangia and pinnules appear to constitute a reliable basis for recognizing this fructification as a small varietal segregate of S. *minor*. The characters of S. *minor* var. *parvifolia* are summarized in the following diagnosis:[15]

Varietal Diagnosis: Synangia borne in a single series on each side of the midrib, and consisting of 4, sometimes 5, sporangia. Sporangia ovate, with blunt apices, averaging approximately .58 mm. in length, .35 mm. in width, closely appressed at the bases, but entirely separate for the greater part of their lengths; outer surfaces of walls thickened, inner surfaces thin; dehiscence by means of a longitudinal cleft along the innermost surface of the sporangial wall. Pinnules with strongly inflexed margins, averaging 3 mm. in length, normally about 1.75 mm. in width but 2.60 mm. if unrolled. Spores round, averaging 15 μ in diameter; walls with triradiate scars and otherwise smooth exines.

Age: Des Moines Series of the Pennsylvanian; the Great Coal Ball Horizon.

Localities: Urbandale Mine, Iowa; Berryville, Ill.; Lynnville, Ind.; Mineral, Kans.; Shore, Lancashire, England.

Type Slides: #1703–1708.

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[15] Graham (1934) described fructifications which correspond exactly with S. *minor* var. *parvifolia* in every aspect. He felt, however, that the size factor was one which could have been induced by environment and referred the specimens to S. *minor*. The constancy of the small size of this variety having been demonstrated by its widespread distribution, it seems probable that the specimens he described should be referred to S. *minor* var. *parvifolia*.

SCOLECOPTERIS **incisifolia**, sp. nov. (text-fig. 1; figs. 34–41).

Several isolated fragments of this fructification, including three nearly complete supporting pinnules, were found in WCB 431, from the Urbandale Mine. While these specimens represent various stages of maturity and accordingly display greater variation of size, it was possible to correlate them by comparisons of the spores and the oddly incised foliage.

In one specimen in which the pinnule is sectioned at right angles to the plane of the lamina and parallel to the midrib (fig. 34), several synangia are seen sectioned transversely. These were apparently preserved prior to spore formation, as neither spores nor lines of dehiscence are noticeable. The extreme thickness of the outer walls of the sporangia is striking as compared to the thin inner walls. Of the four synangia shown here, three are trilocular, the fourth quadrilocular. An inspection of all the specimens available shows the quadrilocular synangia to be slightly more numerous than the trilocular, while synangia with more than four sporangia have not been observed.

In mature fructifications (fig. 41) the sporangia are intimately appressed to each other, with the result that the lateral sporangial walls are flattened while the outer walls are rounded. The inner, or lateral, walls of the sporangia are apparently only a single cell thick; the outer composed of at least two layers of cells. The sporangia shown in this illustration display maximum diameters of about .36 mm., the entire synangium not exceeding .80 mm. in diameter. Although this specimen does not illustrate dehiscence, others have shown it to occur by a longitudinal cleft along the innermost portion of the wall of each sporangium.

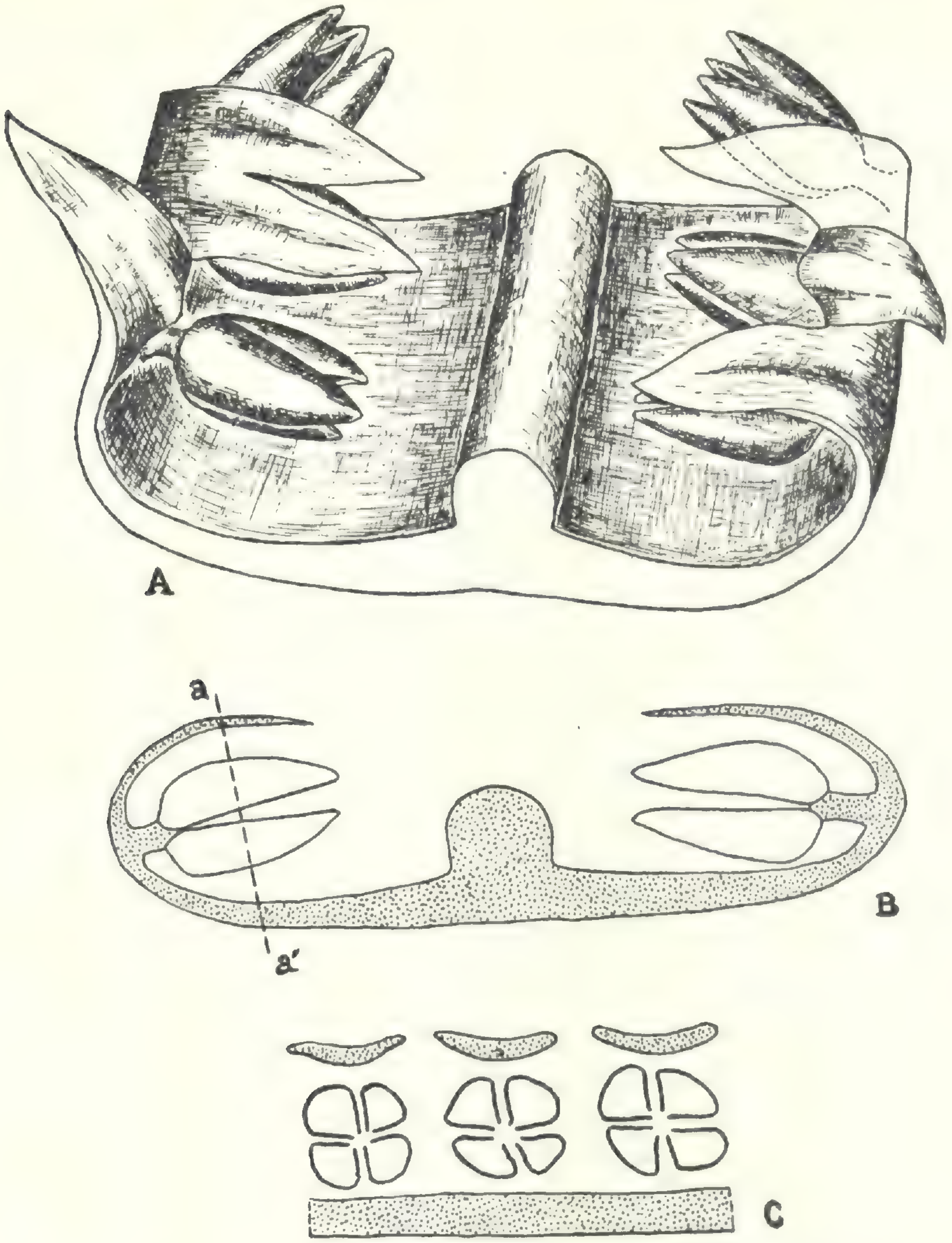
Figure 35 illustrates two immature synangia, sectioned longitudinally, from the same pinnule on which the fructifications shown in fig. 34 were borne. The foliar tissue is seen at the top of the figure and the synangia are attached to it by stout pedicels. The outstanding feature of these pedicels lies in their possession of vascular strands, each consisting of several small tracheidal elements measuring approximately 17–22 μ in inside diameter. These strands originate from the lateral veins of the pinnule, and are the only instances in which vascularization of synangial pedicels has been observed during this investigation. The pedicels shown here are about .22 mm. wide and .30 mm. long. The sporangia, which measure about .45 mm. in length and .17 mm. in width, are attached to the pedicels only by their basalmost portions.

A more mature synangium is shown in fig. 40, in which three sporangia are seen sectioned longitudinally and slightly obliquely. Their shape is roughly ovoid, with no appreciable tapering of the distal end (other specimens, however, show the sporangial apices to be typically more acute). Although the inner walls of the sporangia are closely appressed, this does not represent actual organic fusion, as observations of other specimens have proven the sporangia to be entirely free from each other throughout their lengths. The sporangia of this synangium are .45 mm. in length and .20 mm. in width. Others with lengths reaching .75 mm. have been seen, however.

The spores (fig. 39) are small, reaching 22 μ in length and 14 μ in width. They are of the monolete, bilateral type. The two spores shown here are taken from one of the synangia shown in fig. 41. The spore walls are entirely devoid of tetrad scars or other markings of the exine, and their most conspicuous feature lies in their thickness, most clearly shown in the spore at the left. The spores within a single sporangium vary in length from 18 to 22 μ, and the pronounced thickness of the spore walls usually occurs in only the largest spores, which are interpreted as the most mature.

The major point of interest concerning S. *incisifolia* lies in the supporting pinnules (figs. 37 and 38). Figure 37 shows a pinnule sectioned parallel to the plane of the lamina but slightly beneath it, with the result that only the inflexed marginal portions appear. Since the color contrast between the actual specimen and the surrounding matrix was not great enough to allow for satisfactory photographic reproduction, the accompanying line drawing is offered (fig. 38). This pinnule is 5 mm. long and nearly 2 mm. wide. A portion of the midrib is seen extending proximally for some distance from the distal end. That the margins of the pinnule are strongly inflexed is shown by the fact that the margin at the upper portion of the photograph appears as a continuous line of tissue connecting both ends of the pinnule. Of particular interest here is the undulate *inner* surface of this margin, the outer surface appearing nearly smooth. This results in alternating thick and relatively thin portions of the margin. These are, in fact, the lateral veins, as each thickened portion is seen under high magnification to contain a very small vascular bundle. At point *a*, a single synangium is seen lying in essentially the same plane as the lamina proper. Proceeding now to the opposite margin (lower portion of the illustration), we see that the constrictions of the tissues lying between the veins are further accentuated, and that the margin has become incised at about the center, with two marginal lobes appearing as discrete bodies (point *b* in the line drawing). This fructification resembles S. *latifolia* in that the supporting pinnule has an incised margin, with the fructifications borne near the bases of the lobes.

A correlative inspection of fig. 34 and figs. 37 and 38 shows that the former represents a section taken parallel to the midrib, but very close to the margin and in a plane at right angles to that of figs. 37 and 38. Thus while the synangium seen in figs. 37 and 38 is sectioned longitudinally, those in fig. 34 are transversely sectioned. Here the lamina of the pinnule appears at the upper part of the photograph. Directly beneath this lie the synangia, and below them are the marginal lobes which have been so strongly inflexed that they too are sectioned transversely. It is of importance to note here that *one lobe* lies directly opposite each fructification. These are rather sausage-shaped in transverse section, with the convex surfaces directed toward the synangia. They average 90 μ in thickness and approximately .34 mm. in width. A single lobe, sectioned transversely, is shown in fig. 36. Since sections comparable to the one seen in fig. 17 *(S. latifolia)* have not been found in this material, the length of these lobes is not known. In one instance,



Text-fig. 1. Reconstruction of *Scolecopteris incisifolia: A* shows the gross aspect of the lower surface of a portion of a fertile pinnule; *B*, a transverse section of the pinnule; *C*, a section cut through plane *a-a'* of *B* (this approximates the section illustrated in fig. 34).

however, a lobe has been observed nearly 1 mm. in length. These structures are further illustrated in fig. 41.

Although several specimens of S. *incisifolia* show incision of the foliage essentially like that of S. *latifolia*, the marginal lobes of S. *incisifolia* are more strongly inflexed than those of S. *latifolia*, the tips pointing almost directly toward the midrib of the pinnule. The synangia are inserted one near the base of each marginal

lobe and occupying a position directly beneath a lateral vein. Like the marginal lobes, the synangia are also pointed toward the midrib. The morphology of this fructification is presented in text-fig. 1.

From the standpoint of morphology of the pinnules, S. *incisifolia* appears to be most closely related to S. *latifolia*. However, spore morphology of the two appears sufficient to separate them as two entirely distinct species. Spores of S. *latifolia* are relatively large and trilete, while those of S. *incisifolia* are small and monolete. Furthermore, the thick hypodermal layer and hirsute indument of S. *latifolia* are absent in our species. Also, the sporangial walls of S. *latifolia* are nearly equal in thickness, while those of S. *incisifolia* are noticeably thickened on the outer surfaces.

Of the remaining known species of *Scolecopteris*, S. *Oliveri* is the only other one with monolete spores, and it differs from S. *incisifolia* in the following respects: Its pinnules, although minutely toothed, cannot begin to approach the deeply incised condition of our species; the spores of S. *Oliveri* have rugose exines, while those of S. *incisifolia* are smooth; the hirsute and ramental indument of S. *Oliveri* is lacking in our species. For these reasons, in addition to the difference in dimensions of the fructifications, we feel justified in recognizing our specimens as distinct from S. *Oliveri*.

Although the material upon which this description is based is inferior in preservation to any other described specimens of *Scolecopteris*, and the number of specimens found as yet is not great enough to provide as complete an insight into the morphology as has been realized in the study of other species, the small bilateral spores and the incised foliage comprise a combination of characters not yet known to exist in any other species. For this chief reason, these fructifications appear to constitute a distinctly new species of *Scolecopteris*. The species is named with reference to the margination of the pinnules.

Specific Diagnosis: Synangia consisting of 4, sometimes 3, sporangia reaching .75 mm. in length and .36 mm. in width; sporangia blunt to acute at the apex, attached basally to a stout synangial pedicel, but free above; outer surfaces of walls thicker than the inner; dehiscence by means of a longitudinal cleft along the innermost surface of the wall. Pinnules averaging 5 to 6 mm. in length and 2 mm. in width (exclusive of the strongly inflexed margins); margins deeply incised, with a single synangium inserted near the base of each marginal lobe and directly beneath a lateral vein; lobes averaging .34 mm. in width. Spores monolete, to 22 μ long and 14 μ wide, with thick walls and smooth exines.

Age: Des Moines Series of the Pennsylvanian.

Locality: Urbandale Mine, Iowa.

Type Slides: #1709–1712.

SCOLECOPTERIS **major**, sp. nov. (figs. 42–46).

This description is based upon the fructification content of a single small coal-ball slab from the Urbandale locality. Although the slab originally measured only

approximately 6 × 6 × 1 cm., it was found to contain numerous fructifications which are specifically distinct from other previously described species of *Scolecopteris*, and in an excellent state of preservation. The spores, however, are for the most part poorly preserved, and recognizable foliar remains to which the fructifications might be attributed are entirely lacking.

The synangia are composed of only four sporangia, except in one case where a single synangium with five sporangia was observed. The length of the synangia reaches 3 mm. (including the pedicel). In transverse section the fructifications are roughly circular, attaining diameters of about .90 mm. In all cases, the fructifications, although apparently mature and almost devoid of spores, have maintained a close appression between adjacent sporangia.

The pedicel is short and broad, measuring approximately .35 × .60 mm. in the specimens in which this portion was still intact (fig. 44). It is possible, however, that the length may have been greater, since the actual attachment to foliar tissue has not been observed. The pedicel is not known to contain vascular elements.

Individual sporangia are remarkable for their extreme length. They average more than 2 mm. long, and one specimen has been found which measures 2.9 mm. long. In transverse section they appear much as the four equal segments of a circle, with the two lateral walls of each sporangium creating an angle of approximately 90 degrees. The width of the sporangia is greatest near the proximal ends, reaching .60 mm.; it gently decreases toward the distal ends, resulting in very acute apices (figs. 43 and 44). The outer walls of the sporangium are at least two cells thick, the thickness increasing toward the distal ends. The lateral or inner walls are composed of only one layer of cells, elongate in the direction of the long axes of the sporangia. The cells of the inner sporangial walls have lost their walls on the surfaces facing adjacent sporangia. In this respect the synangia, as seen in transverse section, resembles S. *iowensis* except for the number of sporangia contained. The transverse aspect of the fructifications is illustrated in fig. 42. Here the longitudinal slits of dehiscence may be noted as openings at the innermost portions of the sporangial walls (i.e., at the right angle created by the two lateral walls).

Multicellular hairs reaching 300 μ in length are found on the outer sporangial walls. They are most thickly aggregated at the apices of the sporangia, their number decreasing gradually toward the bases. In fig. 46 two such hairs are seen in high magnification.

The majority of our specimens were preserved after the spores had already been shed. However, several sporangia with portions of their spore masses intact have been found. In general, the spores are round and large for this genus, the diameters ranging from 45 to 55 μ. The exine is characterized by a rather coarse reticulate sculpturing, and triradiate ridges are present in the better-preserved specimens (fig. 45).

COMPARISON OF THE VARIOUS SPECIES OF *SCOLECOPTERIS*

	Average dimensions of sporangia	Number of sporangia per synangium	Nature of sporangial walls	Dimensions of pinnules	Pinnule margins	Arrangement of synangia	Spore dimensions, sculpturing
S. elegans Zenker	.40 × .90 mm.	Usually 5	Thickened outer surfaces; inner surfaces thin	3.50–4.00 mm. long; 1.50–1.70 mm. wide	Entire	Single series on each side of midvein	10 μ diameter; triradiate scars, smooth exines
S. Oliveri Scott	.44 × 1.32–1.40 mm.	Usually 4, sometimes 3 or 5	Thickened outer surfaces; inner surfaces thin	6 mm. long; 2.70 mm. wide	Minutely toothed	Single series on each side of midvein	Bilateral, with greatest dimension 18 μ; exine rugose
S. latifolia Graham	.34–.39 × .90–1.20 mm.	3 or 4	No thickening of outer surface	3.80 mm. long; 7 mm. wide if unrolled	Deeply incised	Single series on each side of midvein	35 μ diameter; triradiate scars, smooth exines
S. Radforthii Andrews	.25 × .70 mm.	3 or 4	?	3 mm. long; 2 mm. wide	Entire	Single series on each side of midvein	32 μ diameter; triradiate scars, smooth exines
S. minor Hoskins	.28 × .70 mm.	Usually 4, sometimes 5, rarely 6	Thickened outer surfaces; inner surfaces thin	6–7 mm. long; 3.30 mm. wide	Entire	Single series on each side of midvein	17 μ diameter; no markings
S. minor var. *parvifolia* Mamay	.35 × .58 mm.	Usually 4, sometimes 5, rarely 6	Thickened outer surfaces; inner surfaces thin	3 mm. long; normal width 1.75 mm.; 2.60 mm. if unrolled	Entire	Single series on each side of midvein	15 μ diameter; triradiate scars, smooth exines
S. iowensis Mamay	.35 × .90 mm.	4, 5, usually 6	Thickened outer surfaces; inner surfaces thin	7 mm. long; normal width 3.5 mm.; 5 mm. if unrolled	Entire	Single *or* double series on each side of midvein	65–80 μ diameter; triradiate scars; reticulate exines
S. major Mamay	.50 × 2.10–2.90 mm.	Usually 4, rarely 5	Thickened outer surfaces; inner surfaces thin	?	?	?	45–55 μ diameter; triradiate scars; irregularly reticulate exines
S. incisifolia Mamay	.33 × .75 mm.	3, usually 4	Thickened outer surfaces; inner surfaces thin	5–6 mm. long; 2 mm. wide (exclusive of the inflexed margins)	Deeply incised	Single series on each side of midvein	Bilateral, 22 × 14 μ; smooth exines

Although associated foliar remains are not distinguishable, these fructifications, judging from their general orientation, seem to have been preserved in their natural position. They are nearly all oriented in the same direction and very closely crowded (fig. 42). For this reason it seems safe to assume that these fructifications, like those of S. *iowensis*, were borne in more than one series on each side of the midrib of the pinnule.

A comparison of S. *major* with the other known species of *Scolecopteris* reveals several significant differences, the most notable one being the size of the sporangia. The species most closely approaching S. *major* in sporangial dimensions is the English species S. *Oliveri* Scott. However, the average difference in length of sporangia is approximately 1 millimeter. In addition, the small bilateral spores of S. *Oliveri*, in contrast to the large trilete spores of S. *major*, lend much further weight to a specific distinction between the two.

Of the remaining species of *Scolecopteris*, none approaches S. *major* in size. The sporangium is up to 1.6 mm. longer than that of any other species, which constitutes a large difference in consideration of the generally small size of the fructifications. In spore size, S. *major* seems to occupy a position intermediate between S. *latifolia* Graham and S. *iowensis*. Although the spores are somewhat smaller than those of S. *iowensis*, from the standpoint of morphology and exine sculpturing, they correspond more closely to those of that species. It seems indeed that the closest relationship of S. *major* lies with S. *iowensis*. As has been previously pointed out, single sporangia of the two species appear extremely similar as seen in transverse section. Furthermore, if the assumption that the synangia of S. *major* were borne in more than a single series on each side of the midvein should ultimately be proven to be a correct one, the relationship between the two species will be materially strengthened. However, the presence of hairs on the fructification, the almost exclusive predominance of synangia with only four component sporangia, and the great size of S. *major* serve as sufficiently distinctive characters to warrant its recognition as a separate species. The specific name S. *major* is proposed, in reference to the large size of the fructifications.

Specific Diagnosis: Synangia consisting of 4, rarely 5, sporangia basally attached to a short pedicel. Sporangia from 2.10 to 2.90 mm. long, averaging .50 mm. in width; outer walls thickened, inner walls thin; dehiscence by means of longitudinal clefts along the inner sporangial wall; multicellular hairs reaching 300 μ in length produced on outer sporangial walls. Spores round, from 45 to 55 μ in diameter, with triradiate ridges and coarsely reticulate exines.

Age: Des Moines Series of the Pennsylvanian.
Locality: Urbandale Mine, Iowa.
Type Slides: #1713–1717.

Eoangiopteris Andrewsii, gen. et sp. nov. (text-fig. 2; figs. 47–53).

The marattiaceous fructifications dealt with thus far in this paper are those which display radially symmetrical arrangement of the sporangia. The opinion expressed by various authors that this type of fructification represents the archetype in the Marattiaceae has indeed been strengthened by the results of this study. There is no apparent reason to doubt the validity of such an opinion, considering the great predominance of radial sori in the Carboniferous rocks in which the oldest known members of the Marattiaceae are found.

At this point it seems desirable to present a cursory survey of the living Marattiaceae from the standpoint of soral morphology. Of the seven living genera of this family, only one produces radial sori *(Christensenia)*. All other living genera produce fructifications which display linear or bilateral symmetry. The predominance of linear sori among the living Marattiaceae, as opposed to the predominance of radial sori among the Carboniferous representatives of the family, poses the following questions: When did the linear sorus first appear on the scene? How did it evolve? It is known that the linear sorus was already well developed by Triassic times (*Danaeopsis* Heer; *Marattiopsis* Schimper), and the presence of the genera *Danaeites* Goeppert and *Parapecopteris* Grand'Eury in the European Coal Measures indicates a very early origin for this type of fructification.

In the genus *Eoangiopteris* we find a fructification with linear arrangement of the sporangia, but with certain characters strongly reminiscent of *Scolecopteris*. Whether or not it represents the actual ancestral type from which the linear sori of certain of the living marattiaceous genera were derived cannot be conclusively stated at this time. It appears to represent a step in that direction, however, and the matter will be discussed in detail in the phylogenetic section at the end of this paper.

Numerous scattered fragments of this fructification have been found in coal balls 437A, 437B, 442, 500, 501, 502, 516, 678, 679, and 680, of the Washington University collection. These coal balls are all from the Urbandale mine. While the majority of the fragments studied consist of only a single sorus, six specimens have been found which contain more or less complete fertile pinnules (WCB 437A, 442, 501, 502, 679).

Although *Eoangiopteris* lacks the predominant radial sori such as found in the fossil genera *Scolecopteris*, *Ptychocarpus*, and *Cyathotrachus*, it agrees structurally with those living marattiaceous genera whose fructifications are linear and free-sporiangiate *(Archangiopteris, Angiopteris,* and *Macroglossum)*.

The number of sori produced by a single pinnule ranges from 12 to 18. They lie closely spaced and parallel to each other on the dorsal surface of the pinnule, extending from the midrib as far as the inflexed margin. Their linear axes create an angle of approximately 40 degrees with the midrib, the angle of divergence from the perpendicular being toward the apex of the pinnule. By serial peels of the specimen found in WCB 442, it has been established that the sori lie directly beneath and parallel to the lateral veins.

The sori are attached to the pinnule by fleshy receptacles (figs. 48, 51) composed of undifferentiated isodiametric cells averaging 75 μ in diameter. Figure 51 represents a sorus sectioned through its long axis in the plane parallel to the long axes of the sporangia; here the receptacle is shown to be approximately half as deep as the length of the sporangia, with the point of attachment to the pinnule somewhat shorter than the total length of the sorus, which ranges from .90 to 1.35 mm. The sori average about .45 mm. in width. The receptacle is not vascularized.

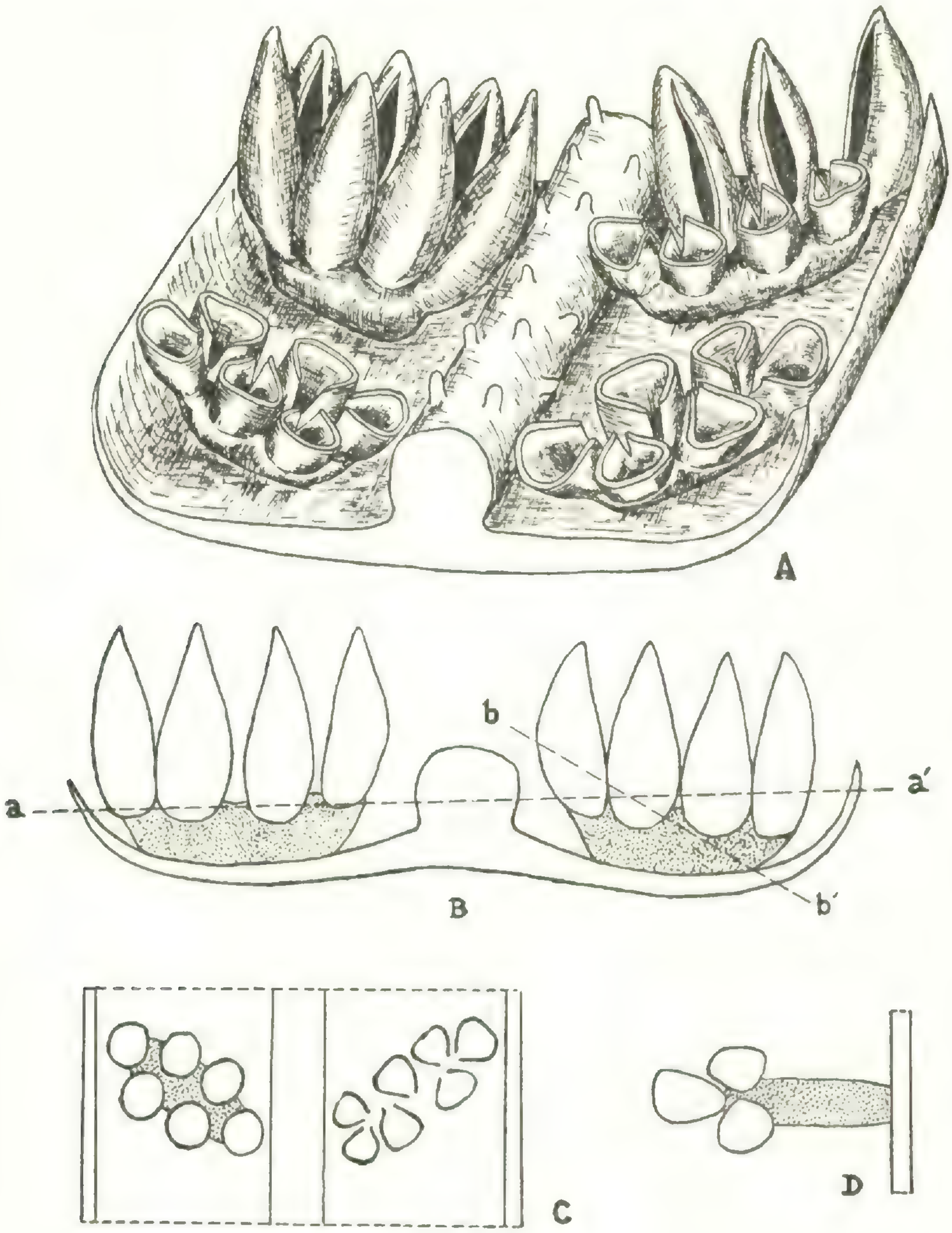
The number of sporangia in the sorus ranges from five to eight, the sori with fewest sporangia being found nearest the distal end of the pinnule. The bases of the sporangia are shallowly immersed in the tissue of the receptacle, but beyond this point of attachment there is no organic connection between adjacent sporangia. A transverse section through the basal portions of the sporangia (fig. 49) shows them to be oval and approximately .25 mm. in diameter, with the receptacular tissue distinguishable between sporangia. A section taken above the point of attachment to the receptacle (fig. 50) shows the sporangia to be roughly triangular in transverse section; in longitudinal section (fig. 51) they are elongate and pyriform, with the greatest width near the point of attachment to the receptacle. In length the sporangia range from .75 to .90 mm., those in the center of the sorus being slightly longer than those at either end. The sporangia of a single sorus are arranged in two rows, each containing up to four sporangia. The rows are either directly opposed or slightly enmeshed in each other, much as the teeth of two gears.

Although preservation of the sporangial walls is not as complete as desirable, it is evident that they are composed of at least two layers of cells. The outermost cells are thick-walled and contain a dense black substance very similar to that observed in the corresponding tissue of *Scolecopteris iowensis*. The inner cell walls are usually thinner than the outer.

Dehiscence (fig. 50) occurs by means of a longitudinal cleft along the innermost wall of the sporangium, the opening extending from the apex of the sporangium to its point of attachment. In details of dehiscence and cellular structure of the sporangial walls the sporangia of *Eoangiopteris* are strongly reminiscent of those of *Scolecopteris iowensis*—so much so, in fact, that single isolated sporangia of the two fructifications would scarcely be distinguishable, discounting the slight discrepancy in size.

Most of the spores are badly crushed, but their salient features have been determined from a few well-preserved specimens. The spores are spherical, with quite thick walls, and range from 45 μ to 60 μ in diameter. The exine shows faint triradiate ridges, but its outstanding feature lies in the nature of the sculpturing. In fig. 52 the exine is seen to be marked by numerous closely spaced, roughly circular pits averaging 4 μ in diameter. The spore output was apparently low, each sporangium having produced a maximum of approximately a hundred spores.

The pinnules range from 7 to 9 mm. in length and from 2.50 to 3 mm. in width. The distal ends are usually somewhat narrower than the proximal. The



Text-fig. 2. Reconstruction of *Eoangiopteris Andrewsii:* *A*, lower surface of a portion of a pinnule with four synangia attached, the two lower synangia having been transversely sectioned; *B*, transverse section through the pinnule and two synangia, receptacle shaded; *C*, left, a section of synangium taken through plane *a-a′* of *B* (approximately same sectional plane as shown in fig. 49); *C*, right, approximately the section shown in fig. 50; *D*, section through plane *b-b′* of *B* (approximately the same as shown in fig. 48).

margins are strongly inflexed, appearing as a more or less continuous line of tissue surrounding the fructifications when seen in sections that have been made in a plane parallel to and below that of the lamina. In the light of our present knowledge of the fossil Marattiaceae we may conclude that these pinnules represent the ultimate divisions of a several-times compound frond belonging to the *Pecopteris* group. Further evidence in support of this opinion is seen in the vascular anatomy of the specimen shown in fig. 53. This represents the midrib of a pinnule, sectioned transversely. The outermost tissue consists of large collenchyma-like cells, with a few outstandingly large ones, possibly of secretory nature, interspersed among them. The inner zone consists of several layers of smaller, thin-walled cells surrounding a horseshoe-shaped vascular strand (fig. 53a) whose open ends point adaxially. The shape of the vascular strand suggests this pinnule to be the ultimate division of a *Stipitopteris* or some closely allied psaronean petiole containing a horseshoe-shaped leaf trace.

A few multicellular hairs, ranging to .20 mm. in length, have been observed on the midrib of the pinnule (fig. 53b).

A reconstruction of *Eoangiopteris* is presented in text-fig. 2.

The linear, free-sporangiate sori of the genus *Grand'Eurya* Stur, from the Permo-Carboniferous of Autun, are quite similar to those of *Eoangiopteris*. In *Grand'Eurya,* however, there is no evidence of a receptacle, the sporangia being sessile on the pinnule. This difference presents a close parallel to the generic difference between *Scolecopteris* and *Asterotheca.*

Only two other linear marattiaceous fructifications are known which closely approximate *Eoangiopteris* in age. They are *Danaeites* Goeppert[16] from the European Coal Measures, and *Parapecopteris* Grand'Eury from the Upper Carboniferous of Gard and St. Étienne. However, their sporangia are laterally fused, while those of *Eoangiopteris* are entirely free from each other. Another major difference is the mode of attachment to the lamina; in *Eoangiopteris* the sori are elevated from the surface of the lamina by a receptacle, while, at least in *Danaeites*, they are sunken within the foliar tissue. These differences correspond closely in magnitude to the generic differences between the fructifications of such living marattiaceous genera as *Danaea* and *Angiopteris.*

A survey of the remaining known linear sori found among the fossils reveals none with which *Eoangiopteris* might be considered congeneric. A superficial examination of the Permian genus *Chansitheca* Rege (for a full account see Halle, 1927), which is known from compressions only, reveals a rather close similarity to *Eoangiopteris,* from the standpoint of general shape and distribution of the sori. *Chansitheca,* however, has sporangia with well-defined annuli, for which reason Halle ascribes to the genus a close affinity with *Oligocarpia* rather than with any marattiaceous entity.

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[16] The generic name implies a relationship with the modern genus *Danaea.* This implication has not met with credence, however, because of the lack of sufficiently detailed illustrations.

The Rhaetic genus *Marattiopsis* Schimper consists of linear fructifications, but here the alliance is obviously one with the modern *Marattia*, since the fructifications consist of two rows of fused sporangia, the whole structure opening much as the shell of a bivalve.

The upper Triassic fructification *Danaeopsis* Heer (also known only as compressions) consists not of fused sporangia, as might be inferred from the generic name, but of two rows of free sporangia extending from the margin to the midrib of the lamina. Discounting the great differences in size of the pinnules and numbers of sporangia in a single sorus, *Danaeopsis* resembles *Eoangiopteris* almost as closely as does the previously mentioned genus *Grand'Eurya*. The salient differences, however, are sufficiently obvious that confusion of the two genera is unlikely.

Among the living Marattiaceae with linear fructifications, the genera *Macroglossum*, *Archangiopteris*, and *Angiopteris* possess free sporangia, in which respect they resemble *Eoangiopteris*. While the fossil record is not yet sufficiently complete to allow us to draw incontestable conclusions as to phylogenetic series in the Marattiaceae, it seems reasonable to consider this fructification as an intermediate form between the Carboniferous radial sorus and the free-sporangiate linear sorus of today as typified by *Angiopteris*. For this reason the generic name *Eoangiopteris* is proposed. The generic and specific characters of *E. Andrewsii* are summarized in the following diagnoses:

Generic Diagnosis: Sori linear, consisting of several exannulate sporangia arranged in two opposed or slightly intercalated rows, and inserted by fleshy receptacles along lateral veins on dorsal surfaces of pecopterid pinnules; sporangia free from each other, with bases slightly sunken in receptacular tissue; dehiscence by longitudinal clefts along inner sporangial walls.

Specific Diagnosis: Pinnules measuring 7–9 × 2.50 to 3 mm., bearing 12 to 18 sori .90 to 1.35 mm. long, with 5 to 8 sporangia per sorus. Sporangia .75 to .90 mm. long, tapering from basal diameters of .20 to .30 mm. to bluntly acute apices; walls generally 2 cells thick. Spores round, with triradiate ridges and measuring 45–60 μ in diameter; exine with circular reticulations approximately 4 μ in diameter.

PHYLOGENETIC CONSIDERATIONS

I. THE PROBLEM: THE ORIGIN OF THE MARATTIACEAE

While the specimens described in the foregoing pages have added to the speciation of known fructification genera, to a clearer understanding of the nature of previously described species, and to the Carboniferous flora of the United States, their significance is not limited to those phases of paleobotany. It is the aim of paleobotany to fill in the numerous gaps in our understanding of plant evolution. The problem of the origin of the Marattiaceae has interested me for some few years, because they seem to have appeared upon the scene very suddenly during the Upper Carboniferous, leaving but few clues as to the nature of their pro-

genitors and the processes involved in their emergence as a well-defined and highly evolved fern group.

The problems of fern phylogeny are most successfully solved through comparative studies of the fructifications. Fortunately there was an amplitude of fructification specimens available for this investigation, and through their study several important points in connection with the phylogeny of the Marattiaceae have been brought to light.

II. THE "PHYLETIC SLIDE"

Studies of the various fern groups have shown that marginal or terminal fructifications are primitive, while those occupying a superficial position are advanced. The "phyletic slide," or migration of the sorus from the marginal to the superficial position, is a phenomenon which is known to occur independently in several groups of living ferns (see Bower, Vol. I, Chap. XII); it entails series of forms which display characters intergrading between the two extremes of soral position. While such series have greatly facilitated the understanding of family relationships, their presence has injected a great measure of difficulty into the task of drawing clear-cut lines of distinction between several of the families. In fact, the net result has been an extremely involved "phyletic bush" (see Bower, Vol. III, p. 2), containing intergrading and poorly defined families, with the Polypodiaceae (representing perhaps the epitome of polyphylesis and "indefinability" when considered as a single "family") occupying the most advanced position. This does not, of course, hold true for all the fern families, for at the base of the "bush", the eusporangiate families (Ophioglossaceae and Marattiaceae) present no difficulties when the "bush" as a whole is viewed. By virtue of their massive exannulate fructifications alone these two families occupy the two basal branches of the "bush"; furthermore, they are readily separable from each other by the position of the fructifications, those of the Ophioglossaceae occupying the primitive marginal position, and those of the Marattiaceae being borne superficially as clearly circumscribed sori, usually synangial. In succeeding pages an attempt will be made to explain the derivation of the superficial position of marattiaceous sori.

III. THE FOSSIL MARATTIACEAE

Marattiaceous fructifications are abundant in American coal balls from numerous localities. The lack of comprehensive and critical studies may be attributed to their small size, and it is very likely that many interesting specimens have been overlooked on this account.

Prior to the discovery of the pteridosperms, paleobotanists treated these fossils as archaic members of the Marattiaceae. Following this important discovery, however, the undeniable likenesses between the fossil and living fructifications came to be considered of less importance than the rather vague supposed likenesses between the marattiaceous fructifications and those presumed to be pteridospermous. Many attempts have been made to link these two unrelated groups upon

insufficient evidence. Kidston (1925) expressed this viewpoint in his exhaustive work on the British Carboniferous flora:

> In *Acitheca*, individual sporangia agree so closely with the microsporangia of *Telangium*, that the affinities of *Acitheca* seem to be Pteridospermous. If, then, this opinion as to the systematic position of *Acitheca* Schimper be correct, I do not see on what ground *Asterotheca* Presl and *Scolecopteris* Zenk. can be excluded from the Pteridosperms.
>
> It would therefore appear that the evidence in support of the occurrence of the Marattiaceous Ferns in Carboniferous times rests on supposition rather than on satisfactory proof. This statement may be thought too strong, but what has been learnt in regard to Pteridospermous microsporangia has undoubtedly weakened the grounds on which the belief in the existence of Carboniferous Marattiaceous Ferns was founded.

EVIDENCE RELATING TO THE MARATTIACEOUS AFFINITY OF THE FOSSIL FRUCTIFICATIONS

1. *A Comparison of Pteridospermous Microsporangiate Organs and Marattiaceous Fructifications.*—

All fructifications suspected of pteridospermous affinity resemble the marattiaceous fructifications *only* in their exannulate and sometimes synangial features (which are also found among the coenopterid fructifications, those of *Stauropteris* and *Chorionopteris* being exannulate, while those of *Corynepteris* and *Chorionopteris* are synangial). Other characters, however, if compared critically, seem to invalidate these similarities as grounds for seriously considering such forms as *Scolecopteris* and others as pteridospermous. These are:

a. Size and Complexity.—While the marattiaceous fructifications rarely attain lengths of more than two millimeters, the majority of the apparently pteridospermous male fructifications (*Dolerotheca, Potoniea, Whittleseya*, etc.) are huge in comparison; there is also a corresponding difference in spore sizes. Furthermore, the marattiaceous fructifications are structurally simple compared to the extremely complex organization of the fructifications mentioned above (see Halle, 1927; Schopf, 1948).

b. Manner in which the Fructifications are Borne.—In all instances where a closer compatibility of sizes can be demonstrated (*Telangium* and *Crossotheca*), the apparently pteridospermous fructifications are borne either terminally (this holds true for the larger forms, also) on naked frond ramifications or marginally on more or less peltate receptacles which terminate the ultimate frond divisions. All the known marattiaceous fructifications, however, are borne superficially on pinnules which show no difference from the sterile ones. *There is no known instance* of a pteridospermous microsporangiate fructification being borne superficially on monomorphic foliage.

c. Associations and Anatomical Evidence.—The following intimate fructification-foliage associations are known to occur: *Crossotheca* and *Sphenopteris* (Andrews and Mamay, 1948); *Goldenbergia* and *Neuropteris*, *Whittleseya* and *Alethopteris*, *Potoniea* and *Neuropteris* (Halle, 1929, 1933); *Dolerotheca* and *Alethopteris* (Schopf, 1948). There is good evidence for the pteridospermous affinity of the foliage genera mentioned above, and while association alone cannot always be held as conclusive evidence, Schopf (1948) has pointed out significant histological similarities between *Dolerotheca* fructifications and *Medullosa* stems

and petioles. On the other hand, *Pecopteris* foliage, upon which the marattiaceous fructifications are borne, is known to occur in intimate association with *Psaronius* stems. Furthermore, the u-shaped vascular strands of the pinnules upon which these fructifications are borne suggest them to be ultimate divisions of a stipitopterid psaronean petiole.

2. *A Comparison of Fructifications of the Living and Fossil Marattiaceae.*—

The following significant points of similarity are demonstrated by a comparison of the living and fossil members of this family:

a. There is a close similarity in sizes of the fossil and living fructifications and spores.

b. In both the living and fossil Marattiaceae, the fructifications are in the form of definitely circumscribed sori, either free-sporangiate or synangial, radial or linear. The similarities between *Ptychocarpus* (fossil) and *Christensenia* (living) and between *Eoangiopteris* (fossil) and *Angiopteris* (living) are much closer than any which can be demonstrated between the fossil marattiaceous sori and any supposedly pteridospermous fructifications.

c. In both the living and fossil Marattiaceae the sori are restricted to a superficial position, and the foliage is monomorphic (only in the living genus *Danaea* is there anything approaching the dimorphic condition).

d. *Psaronius* stems, which are frequently found in intimate association with fertile *Pecopteris* foliage, show a close anatomical similarity to the living marattiaceous genus *Angiopteris*, and cannot be confused with any known pteridospermous stem. Furthermore, the u-shaped trace of the psaronean petiole *Stipitopteris* is quite similar to the traces found in fertile pecopterid pinnules.

It is my opinion that the foregoing evidence, if carefully considered, should lead to the conclusion that the existence of a well-defined group in the Paleozoic, corresponding in a remarkable fashion to the living Marattiaceae, cannot be reasonably denied. Furthermore, efforts made in respect to this group should be directed toward the solution of problems bearing upon their poorly understood phylogeny rather than attempting to correlate them with the pteridosperms on slender threads of evidence.

IV. A PROPOSED EXPLANATION OF THE ORIGIN OF THE MARATTIACEAE

The following facts with reference to the fossil Marattiaceae become increasingly important:

1. The fossil fructifications are essentially identical with the living ones; evolution of the fructifications had apparently reached its peak during late Paleozoic times and then leveled off.

2. The superficial position of the sorus, considered to be the climactic evolutionary result, had been well established in the Marattiaceae by Upper Carboniferous times.

Tentatively accepting the Marattiaceae as derivatives of some branch of the coenopterids, it seems likely that various stages in the migration of the sorus to

the superficial position might be sought in the coal balls, since the two groups were contemporaneous during at least part of their respective geological histories, and fructifications of both groups are frequently found within the same petrifaction. In searching for intermediate forms, then, we would look for either coenopterid fructifications showing tendencies toward the marattiaceous types (massive sporangial walls, synangia, or otherwise closely circumscribed sori) and occupying a terminal or marginal position, or for marattiaceous fructifications occupying marginal or only slightly superficial positions on the lamina.

A. A Review of Coenopterid Soral Morphology

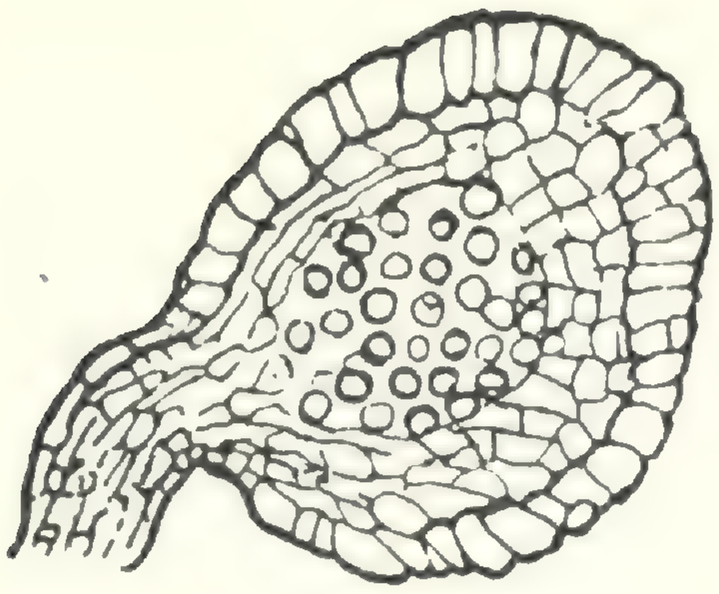
In the following brief review of the outstanding aspects of some of the known coenopterid fructifications, we shall follow the sequence which Bower (Vol. II, p. 39) suggests to represent a line of soral evolution among the coenopterids.

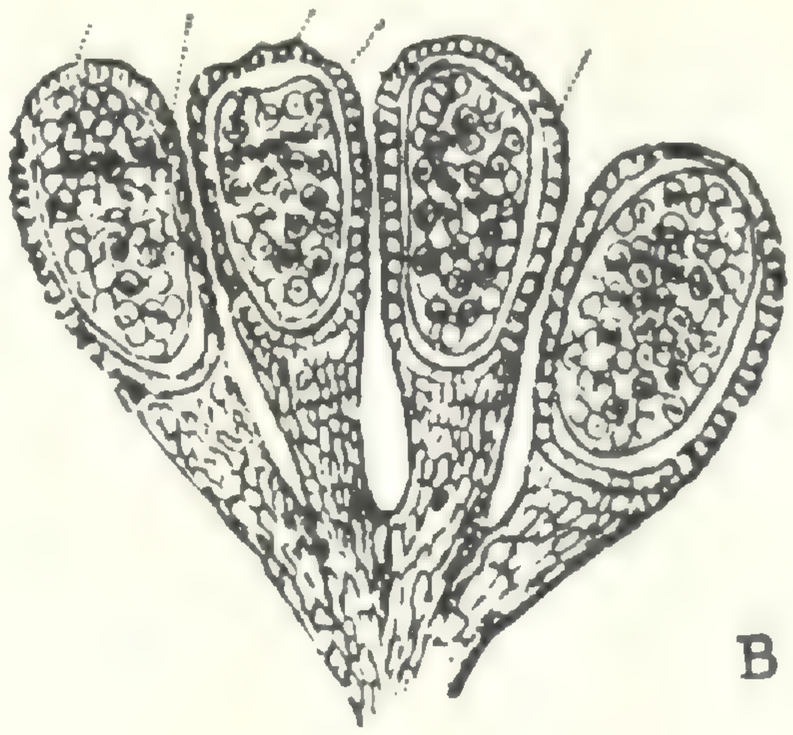
Beginning with the simplest type of fructification, that of *Stauropteris* (see text-fig. 3A), we see that the sporangia are massive-walled, exannulate structures which are borne singly, each occupying the terminal position upon an ultimate ramification of the plant, much in the same manner as the sporangia of *Rhynia*. Continuing with the series, the sporangia of the fructification *Etapteris* (*B* and *C*) appear singly in the terminal position, but are arranged into rather lax tassel-like groups, each group suggesting a derivation from a *Stauropteris*-like progenitor by the aggregation of several individual sporangia. Although this concept is somewhat confused by the appearance of a rather well-developed annulus in *Etapteris*, the chief significance lies in the apparent tendency of the sporangia to become condensed into more intimate association with each other. A further continuation of this tendency may be seen in the genus *Corynepteris (D* and *E)*, in which the sporangia possess annuli much like those of *Etapteris*. However, the condensation of the sporangia has been furthered to the extent that well-defined sori are present in which the sporangia are closely appressed. The sori are borne upon the margins of narrow pinnules. This is the first appearance of a lamina in this series.

The culmination of the tendencies shown in this series appears in the fructification *Chorionopteris (F* and *G)*. Although this fructification has been reported but once, enough is known of its structure to afford the following significant facts:

1. The fructifications are massive-walled synangial groups of four sporangia each, with a continuous sheath surrounding the entire structure.

2. The fructifications are borne singly at the terminations of the lateral veins of a narrow, fleshy pinnule; the pedicels and synangial walls were originally described as "continuations of the tissues of the lateral veins." The synangia are seen to extend from the tips of the foliar lobes; they may thus be termed either *marginal* or *terminal*, depending upon whether the reference is made to the lamina or veins.



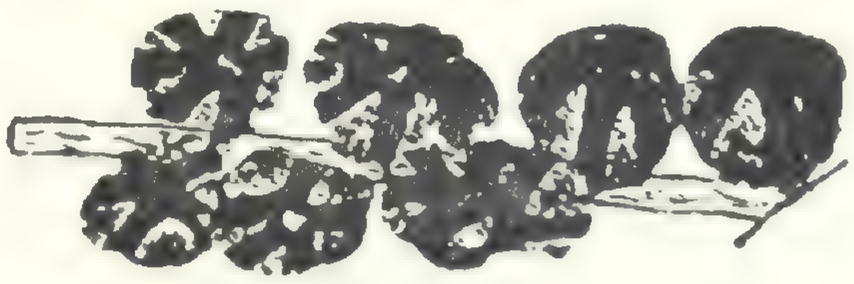


B

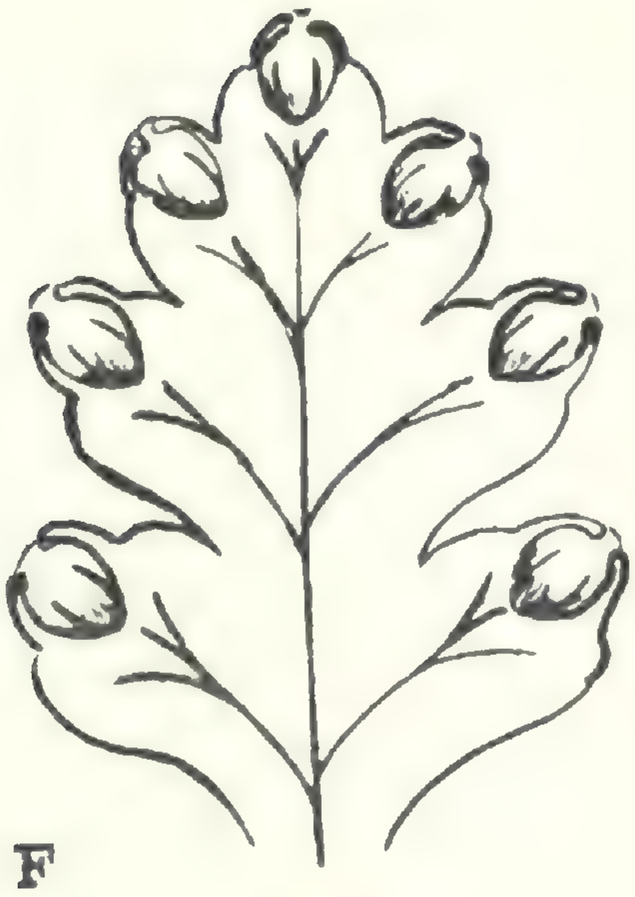
A

C

D



E



F

G

Text-fig. 3. *A*, *Stauropteris Oldhamia* Binney, from Bower, after Mrs. D. H. Scott (approx. × 50); *B*, *C*, *Etapteris* sp., from Bower, after Renault (*B*, approx. × 10, *C*, approx. × 20); *D*, *Corynepteris Essenghi* Andrae, from Bower, after Zeiller (approx. × 10); *E*, *Corynepteris coralloides* Gutbier, from Bower, after Zeiller (approx. × 5); *F*, *G*, *Chorionopteris gleichenioides* Corda, from Hirmer, after Kubart (*F*, approx. × 9, *G*, approx. × 20).

Although the fact that both annulate and exannulate sporangia are involved in the above series seems to cast doubt upon its validity as a single natural sequence, its value lies in the apparent tendency of the fructifications to become aggregated into compact groups which are ultimately borne on the margin of a distinct lamina. It appears that the genera *Stauropteris* and *Chorionopteris*, with their exannulate, thick-walled sporangia, represent the opposite extremities of one line of development within the coenopterids, which leads to the Marattiaceae. The intermediate members of this line are as yet unknown. The genus *Corynepteris*, on the other hand, seems to represent a stage in still another series involving annulate sporangia, which may have culminated in a gleicheniaceous form such as *Oligocarpia*. Information concerning the development of the lamina in these genera is totally lacking.

B. A "PHYLETIC SLIDE" SERIES

Referring back to the fructification *Chorionopteris*, its salient features seem to fulfill the qualifications for a progenitor of the Marattiaceae.[17] The synangia would be easily confused with a scolecopterid fructification if their relationship with the coenopterid petiole *Anachoropteris* were not known. The sporangia of *Chorionopteris* are enclosed by a continuous synangial wall, a feature which is by no means absent in the pecopterid fructifications. It is found in the genera *Cyathotrachus* and *Ptychocarpus*, and in young synangia of *Scolecopteris incisifolia* (fig. 34). Since the chief difference between *Scolecopteris* and *Chorionopteris*, then, lies in their relative positions on the lamina, we are faced with the problem of demonstrating stages intermediate between the marginal and superficial positions. The species *Scolecopteris incisifolia* and S. *latifolia* appear to represent such intermediate stages; the evidence points toward migration of the sorus to the superficial position in which *proliferation* of the upper tissues of the margin of a chorionopterid pinnule produced one like that upon which the two mentioned species of *Scolecopteris* were borne.

The reader is now referred to text-fig. 4, in which a series of diagrams representing marginal portions of fertile pinnules is presented. In *A (Chorionopteris)*, the synangial points of attachment are seen at the tips of the marginal lobes of the pinnule, each one terminating a lateral vein. In *B* (hypothetical) the marginal tissues have proliferated slightly; the inter-lobal embayments of the lamina are still comparatively wide; but the synangial points of attachment are now slightly superficial. In *C* (hypothetical), the proliferation has continued, and the lateral veins have extended slightly beyond the points of attachment of the synangia. *D* represents a stage approximating the condition found in *Scolecopteris incisifolia*

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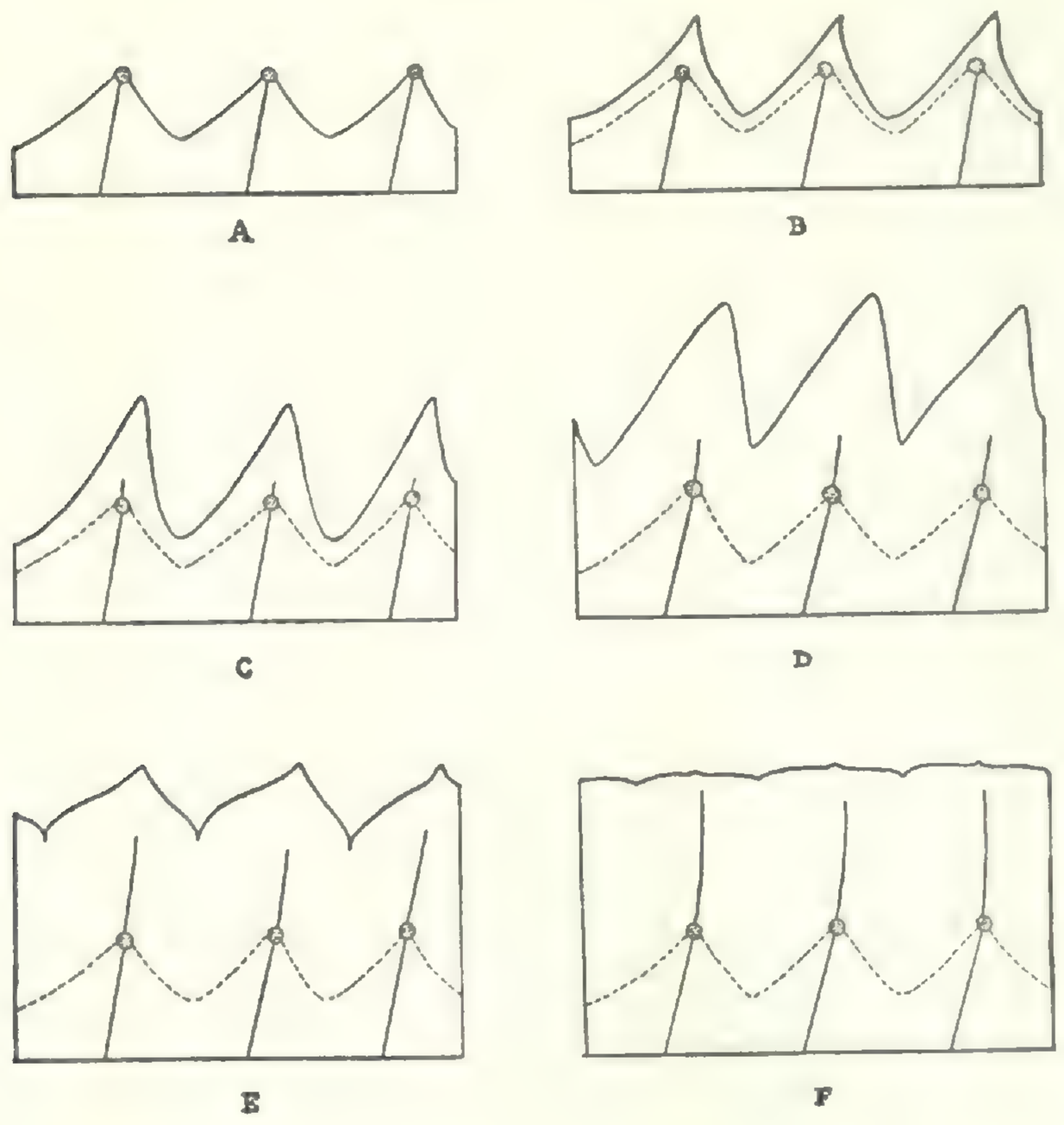
[17]Bower (Vol. II, p. 39) states, in reference to *Chorionopteris:* "A 'phyletic slide' of the sorus to the lower surface of a widening leaf segment . . . . would then give a soral state similar in structure and position to that seen in the Marattiaceae."



Text-fig. 4. Illustrating a possible "phyletic slide" series, beginning with the coenopterid fructification *Chorionopteris* and resulting in the marattiaceous fructification *Scolecopteris*. Shaded circles represent the points of insertion of the synangia; broken lines the original foliar margin shown in *A*.

(compare with text-fig. 1) and *Scolecopteris latifolia*. The lobes are now proportionately longer than wide, and the embayments of the lamina are quite narrow. The synangia are inserted near the bases of the marginal lobes and the ends of the lateral veins, and are now quite superficial in position. In *E* (hypothetical) the lobes have undergone lateral fusion to some extent, a process which is culminated in *F*, in which the margin of the pinnule is essentially entire. This would correspond to the condition seen in *Scolecopteris iowensis* or S. *minor*.

Such a series may also be seen in the ontogeny of various genera of the living Schizaeaceae. The young sporangia begin their development in a marginal position, to be followed by a proliferation of the upper tissues of the margin of the lamina, causing the matured sporangia to assume a superficial aspect. This may represent the ontogenetic reflection of a phylogenetic series such as diagrammed in text-fig. 4, but involving annulate sporangia.

As seen in fig. 17 *(Scolecopteris latifolia)*, the tissues composing the long, narrow marginal lobes seem quite definitely to be direct continuations of the upper epidermal and hypodermal tissues which are characterized by their dense black

cellular contents. This aspect may be best seen in fig. 22, a transverse section of a single lobe. Although the lobes are quite discrete bodies, they are very closely crowded, and it appears that their lateral fusion to form a continuous-margined lamina such as that upon which S. *iowensis* was borne, would present little evolutionary difficulty. Thus the genus *Scolecopteris* is seen to contain forms *(S. latifolia* and S. *incisifolia)* which are intermediate between the marginal and superficial conditions.

There yet remains one puzzling aspect of this hypothesis. Among the coenopterid fragments present in American coal balls, the petiole *Anachoropteris,* which is known to have borne *Chorionopteris* fructifications, is found in numbers exceeded only by fragments of *Botryopteris.* However, fructifications which compare in detail with the original descriptions and illustrations of *Chorionopteris* still remain to be discovered in our petrifactions. Furthermore, although the stems upon which *Anachoropteris* petioles were borne are still unknown, the comparatively large size of the petioles suggests an origin from a stem of such magnitude that it could hardly escape notice. What then are we to deduce from the total absence of stems and fructifications in floras so rich in petiolar fragments? The following suggestions are offered for consideration:

1. The close fundamental resemblances between *Chorionopteris* and various of the scolecopterid species suggests that they compose an evolutionary complex of intergrading forms, and any or all of the intermediate forms presented in the series shown in text-fig. 4 might be sought within either genus. The generic distinction would then depend upon the vascular anatomy of the supporting petiole.

2. *Anachoropteris* petioles, when seen in transverse section, display vascular strands with similar structure to those of the psaronean petiole *Stipitopteris,* with the exception of the position of the protoxylems. They may in all likelihood be ultimately proven to be borne on *Psaronius* stems or upon stems of intermediate structure between *Psaronius* and certain coenopterid stems.[18]

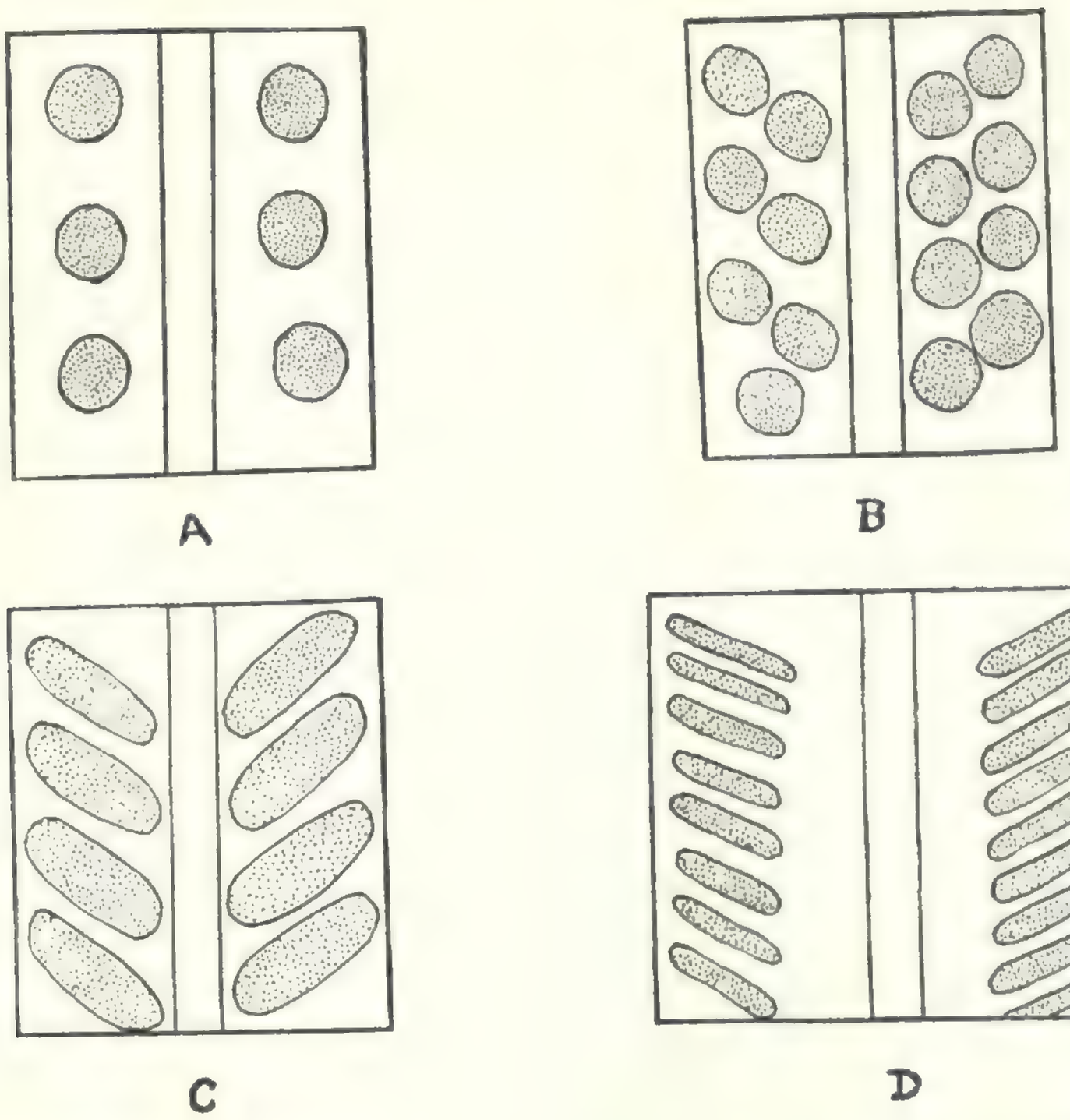
While the hazards of basing conclusions on the association of plant fragments are fully realized the bulk of the evidence uncovered to date strongly indicates a derivation of the fossil Marattiaceae from the anachoropterid coenopterids, involving the migration of the sori from the marginal to the superficial position, as diagrammed in text-fig. 4.

V. EVOLUTIONARY POSSIBILITIES AMONG THE MARATTIACEAE

A. The Derivation of Linear Sori

Upon the basis of the evidence uncovered during this work, we shall now consider the evolutionary possibilities within the Marattiaceae. One of the chief remaining problems lies in the derivation of the linear sorus, now predominant among the living Marattiaceae. Referring back to the description of *Scolecopteris*

[18] Lenz (1942) wrote: "This paper is intended as a further contribution to the apparent relationship between petioles described as *Anachoropteris* and *Stipitopteris* and fern stems described as *Psaronius* and *Caulopteris.*"



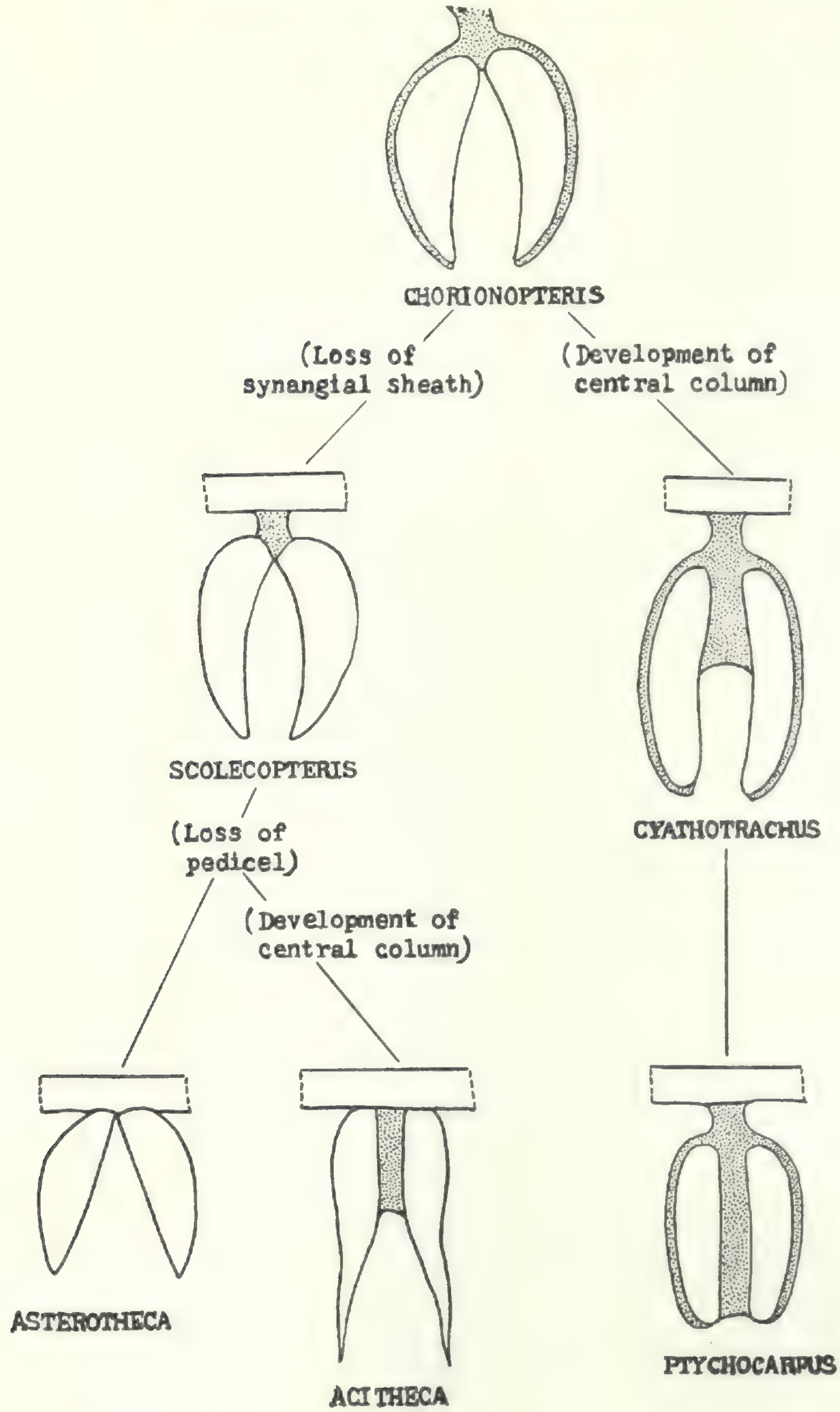
Text-fig. 5. Illustrating a possible sequence in the evolution of marattiaceous fungi: *A*, a typical asterothecous fructification, with the usual uniseriate condition; *B*, in which *two* rows of sori are borne on each side of the midrib, (sometimes seen in *Scolecopteris iowensis*); *C*, linear sorus such as in *Eoangiopteris* resulting from fusion of crowded radial sori such as shown in *B*. Expansion of the lamina might produce either of the two conditions: *D*, in which the sori are situated near the margins and away from the midrib (as in *Angiopteris*); or *E*, partial fission of the linear sori (sometimes seen in *Danaea*). Further expansion and fission might result in irregularly distributed radial sori as seen in *Christensenia (F)*.

iowensis, a radial sorus, and *Eoangiopteris Andrewsii*, a linear sorus, certain similarities may be noted between the two fructifications. Individual sporangia of the two are similar in size, shape, and their dehiscence mechanisms. The tissues comprising the pedicel of S. *iowensis* and the receptacle of *E. Andrewsii* are alike. The spores of the two compare closely in gross morphology, size, and sculpturing of the exine. The chief difference between the two lies in the radial aspect of one as opposed to the linear aspect of the other.

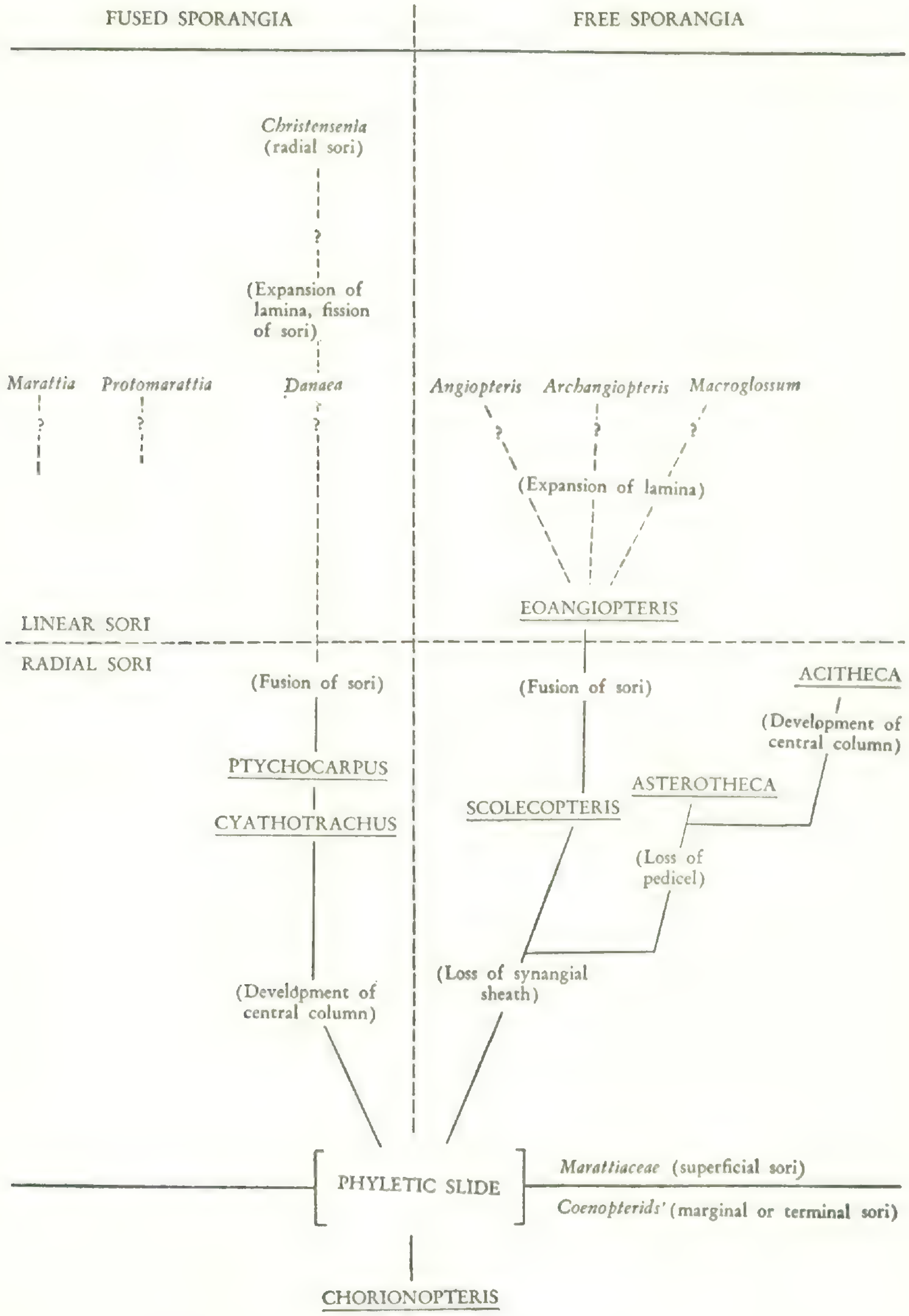
One feature of S. *iowensis* that deserves particular comment is that the fructifications are sometimes borne in *more than a single series* on each side of the midrib, resulting in an extremely crowded condition, as compared with the usual uniseriate arrangement found in other species. This suggests an ultimate *fusion* of sori along a lateral vein; eventual fusion of the pedicels would result in a linear, receptacular sorus such as that of *E. Andrewsii*. This process would allow for an increased sporangial production and more efficient utilization of the limited space provided by as small a pinnule as that which bore *E. Andrewsii*. While it is difficult to make a concrete statement concerning the evolutionary position of S. *iowensis* within the genus, its low spore output points to an advanced position among the known species, and it seems that this is in support of the *fusion* hypothesis offered above.

While it seems possible that *Eoangiopteris* was derived by *fusion* of radial sori and may have given rise eventually to the modern free-sporangiate linear sori of *Angiopteris*, *Archangiopteris*, and *Macroglossum*, the origin of the modern linear sori with fused sporangia remains in doubt. Conceivably the sori of *Danaea* may have evolved by a similar fusion of synangia of the *Ptychocarpus* type; an accompanying loss of the pedicel would result in a sorus similar to that of *Danaea*.

An interesting circumstance is to be noted in the relationship between pinnule size and fructification morphology. While the fossil fructifications were borne on very small, narrow pinnules and were crowded very closely together, the living Marattiaceae have relatively large, wide foliar segments with numerous but uncrowded sori. While the fossil sori are predominantly radial, the living ones are predominantly linear; thus it seems that the expansion of the lamina was accompanied by the development of linear fructification morphology, that is, *to a certain extent*. In this connection it is especially interesting to note that the modern genus *Christensenia*, considered to be the most advanced of the Marattiaceae by virtue of its dorsi-ventral habit, small size, large scales, highly expanded foliar segments and reticulate venation, produces *radial sori* which are very similar to the fossil sorus *Ptychocarpus*. Bower (1923) contends that the radial sori of *Christensenia* have been derived through the fission of a linear sorus of the *Danaea* type, accompanying an expansion of the lamina. Thus, if the proposed hypothesis of *soral fusion* may be considered a reasonable one, it appears that evolution of the marattiaceous sorus has undergone a complete reversal, with the archaic progenitors and most recent derivatives displaying essentially the same sort of soral morphology. This evolutionary sequence is diagrammed in text-fig. 5.



Text-fig. 6. Showing two possible lines of derivation of asterotheceous fructifications. Beginning with the coenopterid fructification *Chorionopteris*, the line of development shown at the right involves development of a central column and results in asterothecous sori with *fused* sporangia. The line of development shown at the left involving loss of the synangial sheath, loss of the pedicel, and development of a central column, results in asterothecous sori with *free* sporangia.



Text-fig. 7. A proposed phyletic chart of the Marattiaceae.

B. The Derivation of the Various Radial Sori

Returning to the fructification *Chorionopteris*, it appears that as a progenitor for the asterotheceous fructifications, only a few minor evolutionary alterations are necessary to produce the latter several types. These fall into two distinct lines (see text-fig. 6).[19] Although *A*, *B*, *C*, and *D* involve free-sporangiate sori, while *E* and *F* represent sori with fused sporangia, a complete series such as illustrated might have been accomplished within either the fused- or free-sporangiate soral groups.

1. By retention of the pedicel and synangial sheath, along with the development of a central column, the *Ptychocarpus* type might be produced, with *Cyathotrachus* as an intermediate.

2. By reduction of the synangial sheath, the *Scolecopteris* and *Asterotheca* types might be derived, depending upon the simultaneous retention or reduction of the pedicel. By the development of a central column in a fructification of the *Asterotheca* type, an *Acitheca*-like fructification might be derived.

The above evolutionary processes, along with that presented in text-fig. 4, would result in the above-mentioned soral types, in the superficial position. It thus appears that pedicellate sori with fused sporangia represent the most primitive type, with sessile, free-sporangiate forms advanced. (This is in direct opposition to the series proposed by Graham (1934), in which sessile forms are considered to be primitive.)

The Marattiaceae are proposed as having been derived from the coenopterid ferns, involving a "phyletic slide" in which the coenopterid genus *Chorionopteris* is the primitive form (text-fig. 4). The superficial marattiaceous sori appear to have developed along two distinct lines: those with fused sporangia placed at the left of the vertical broken line, and those with free sporangia at the right (text-fig. 6). Within each of these two groups are found both the primitive *radial* sori (placed below the horizontal broken line) and the apparently derived *linear* sori (above that line). Although *Christensenia* produces radial sori, it is apparently the most highly evolved form and consequently occupies the highest position among genera with fused sporangia. All fossil genera are underlined in this chart. While future work in the field of coal ball research will undoubtedly modify the phylogenetic trends suggested in the foregoing pages and diagrammed in text-fig. 7, such discoveries are eagerly awaited by the author with the hope that they will greatly amplify our knowledge of the past history of this interesting group of ferns. Any criticisms or suggestions will be gratefully accepted.

Acknowledgment

The author wishes to express appreciation of the many valuable suggestions of Dr. Henry N. Andrews, under whose direction the present work was accomplished. Thanks are also due the Director of the Missouri Botanical Garden for making

[19] Because of its apical annulus, the genus *Sturiella* is of doubtful affinity and is not considered here.

available the library facilities, and Dr. Rolla Tryon, for offering constructive suggestions during the course of this work.

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EXPLANATION OF PLATE

PLATE 1

Figs. 1–4. *Botryopteris fecunda*

Fig. 1. A group of three sporangia, sectioned longitudinally. The pedicel of the sporangium at the left may be seen at the top of the figure. Slide #1680, × 100.

Fig. 2. Two sporangia, sectioned transversely. Note the annulus-like differential thickening of the sporangial walls. Slide #1680, × 120.

Fig. 3. A group of closely crowded sporangia, sectioned both transversely and longitudinally. Slide #1680, × 53.

Fig. 4. Spores. Note the tetrahedral shape and triradiate ridge. Slide #1680, × 700.

Figs. 5, 6. *Botryopteris spinosa*

Fig. 5. Spore. Note the blunt spine-like projections. Slide #1683, × 500.

Fig. 6. A group of loosely aggregated sporangia, sectioned both transversely and longitudinally. Slide #1683, × 45.

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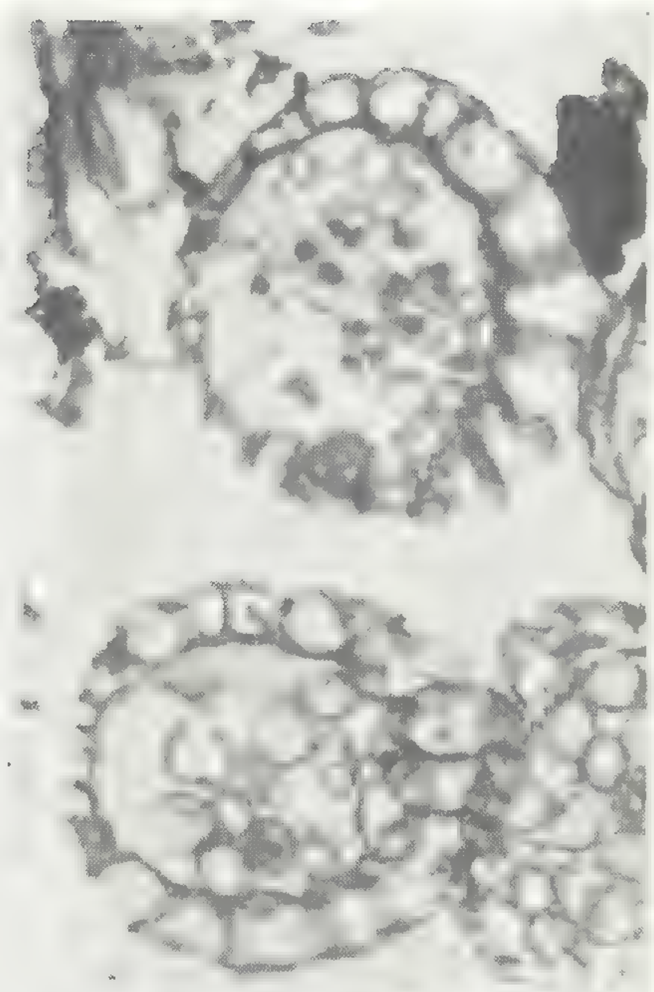

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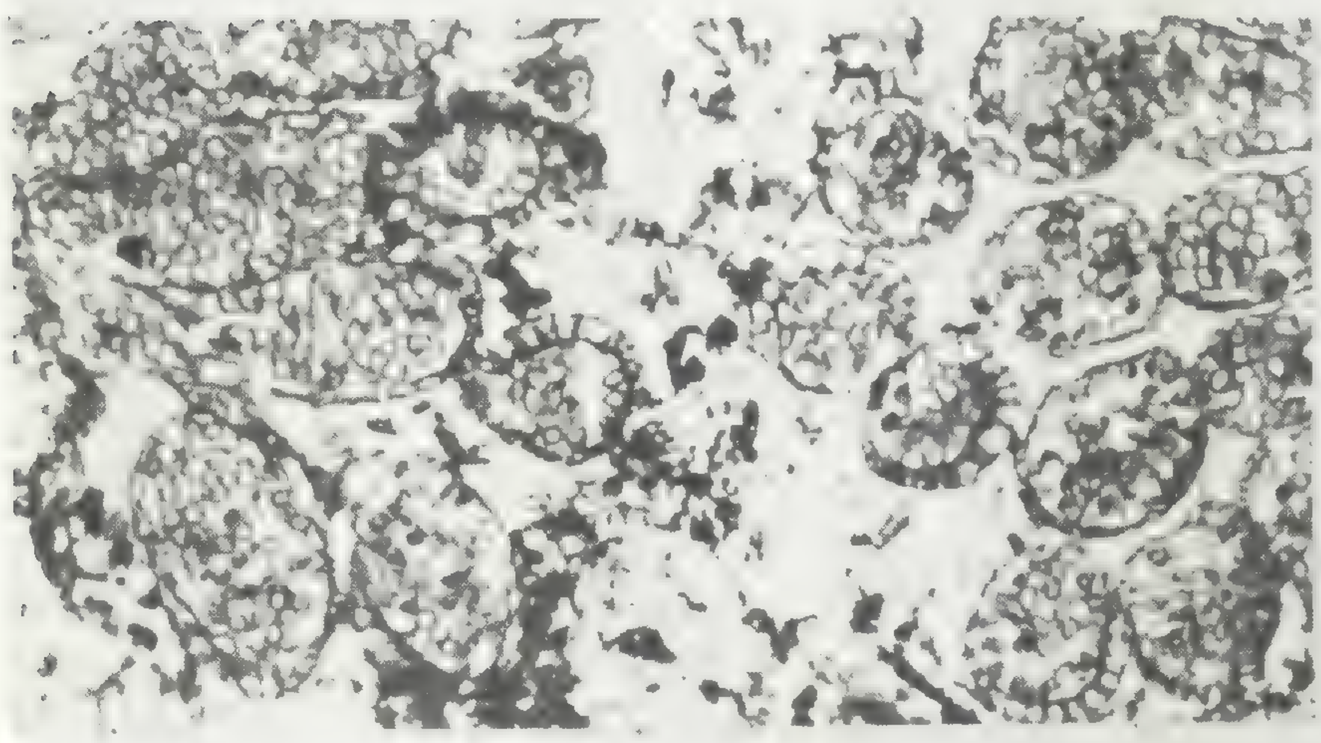

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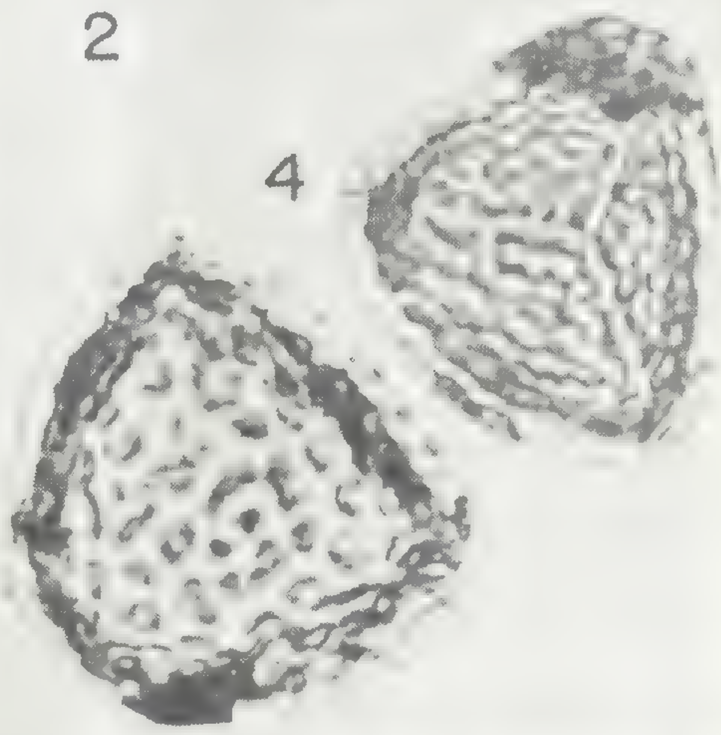

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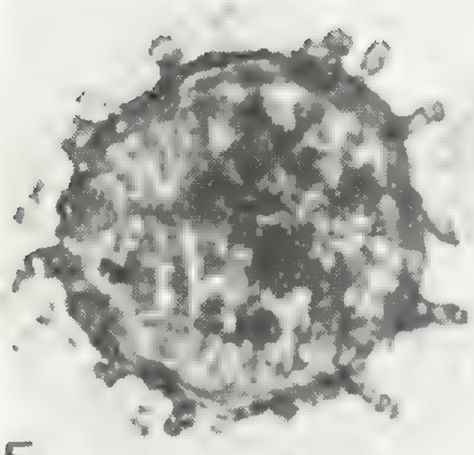

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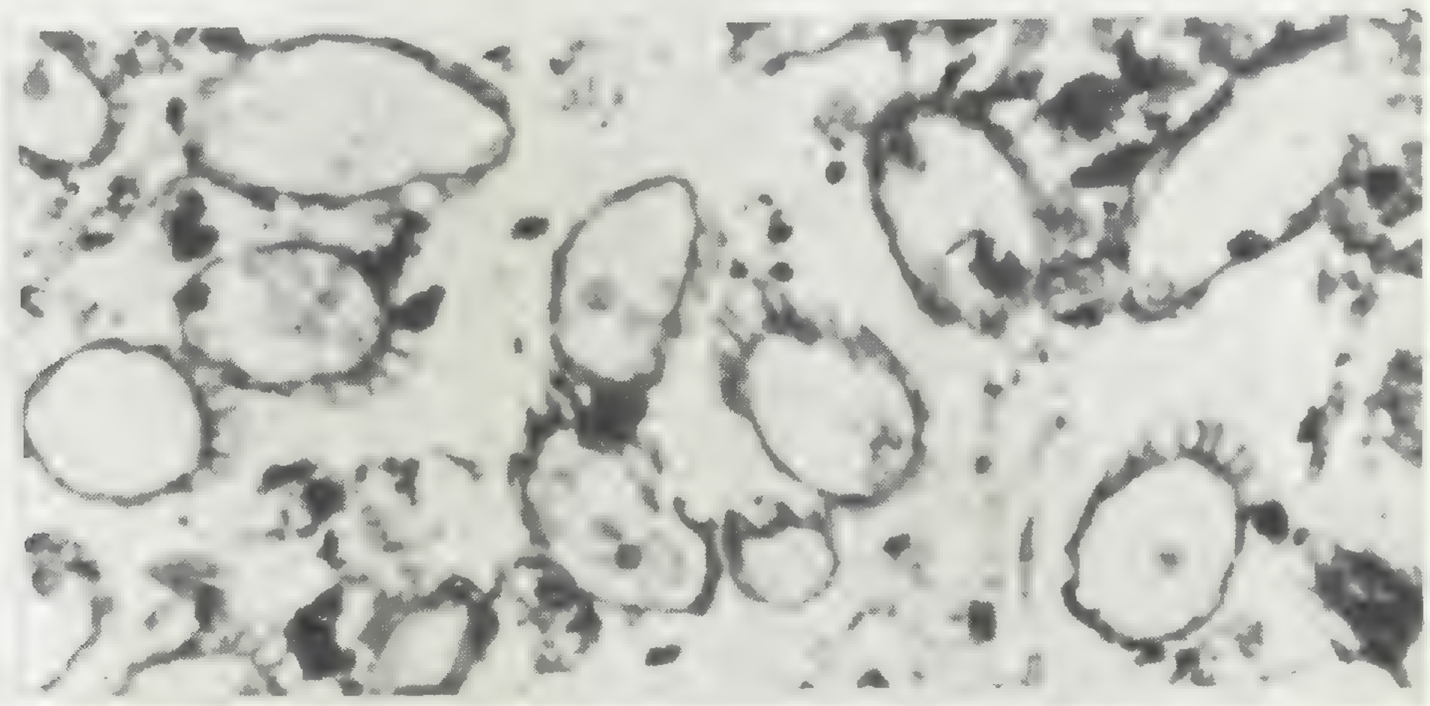

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EXPLANATION OF PLATE

PLATE 2

Figs. 7, 8. *Botryopteris spinosa*

Fig. 7. A group of sporangia, the largest one sectioned longitudinally. Note the short pedicel at the upper right. Slide #1683, × 135.

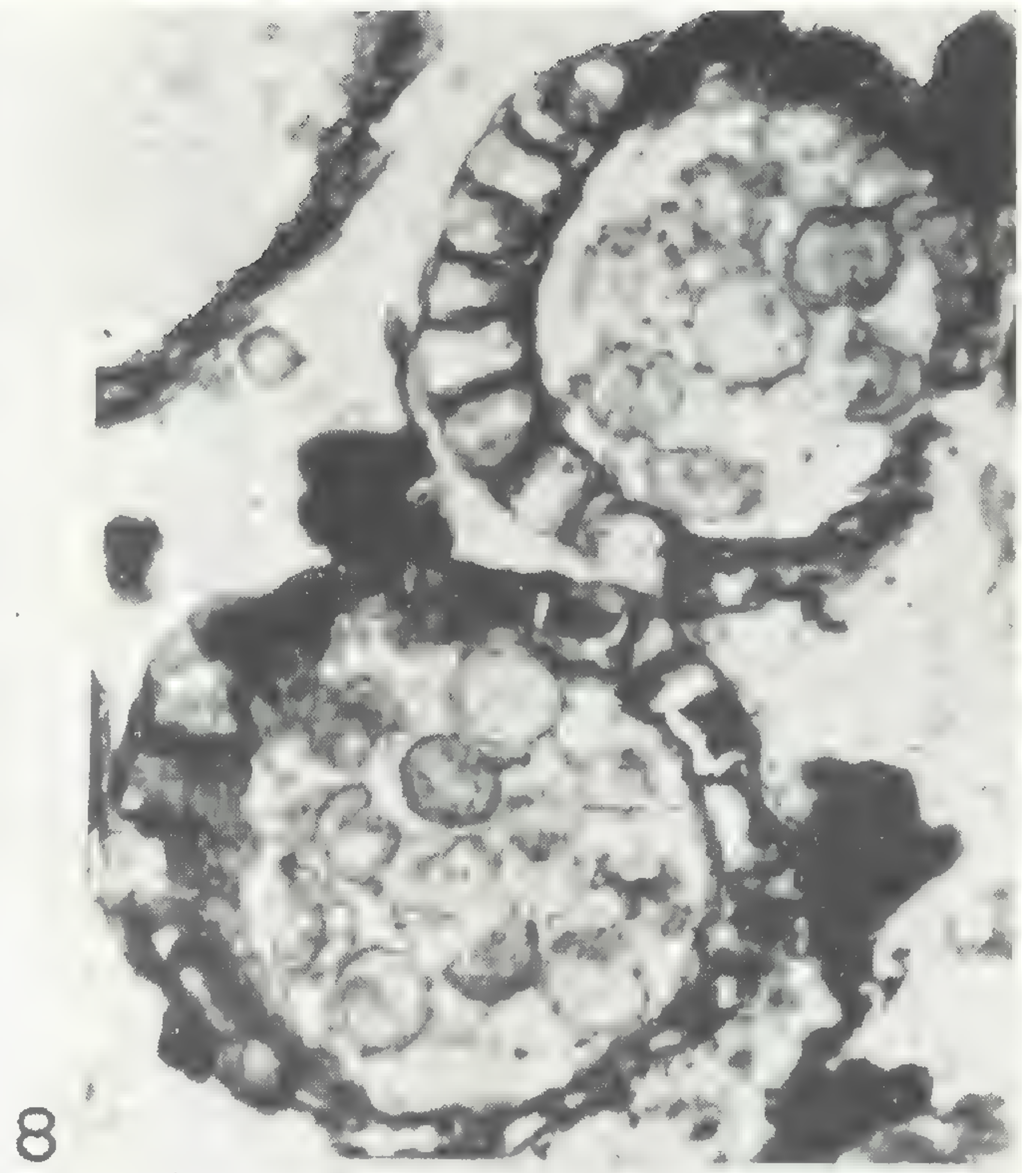
Fig. 8. Two sporangia, sectioned transversely. Note the thin sporangial walls, with annulus-like thickenings. Slide #1683, × 155.

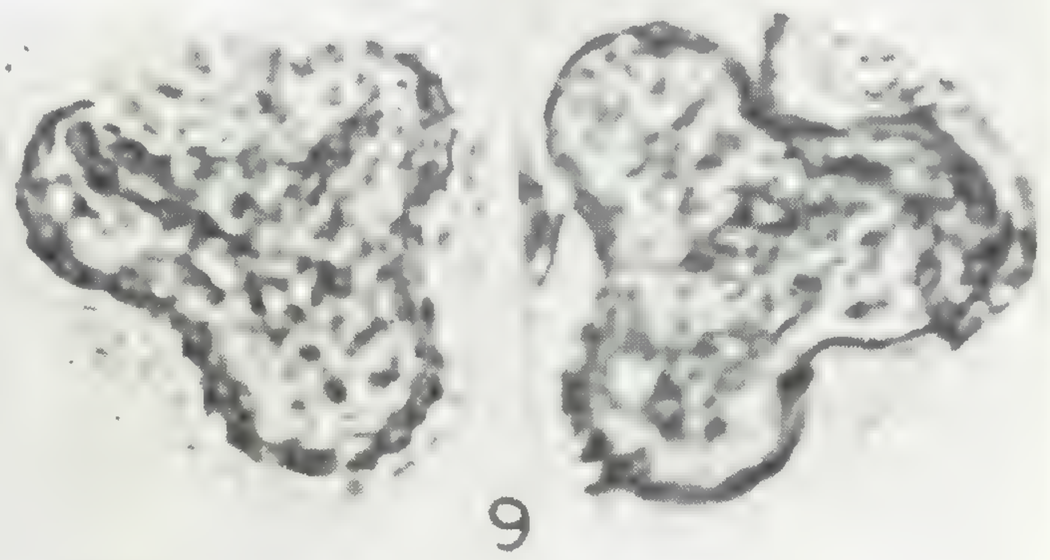
Figs. 9, 10. *Botryopteris illinoensis*

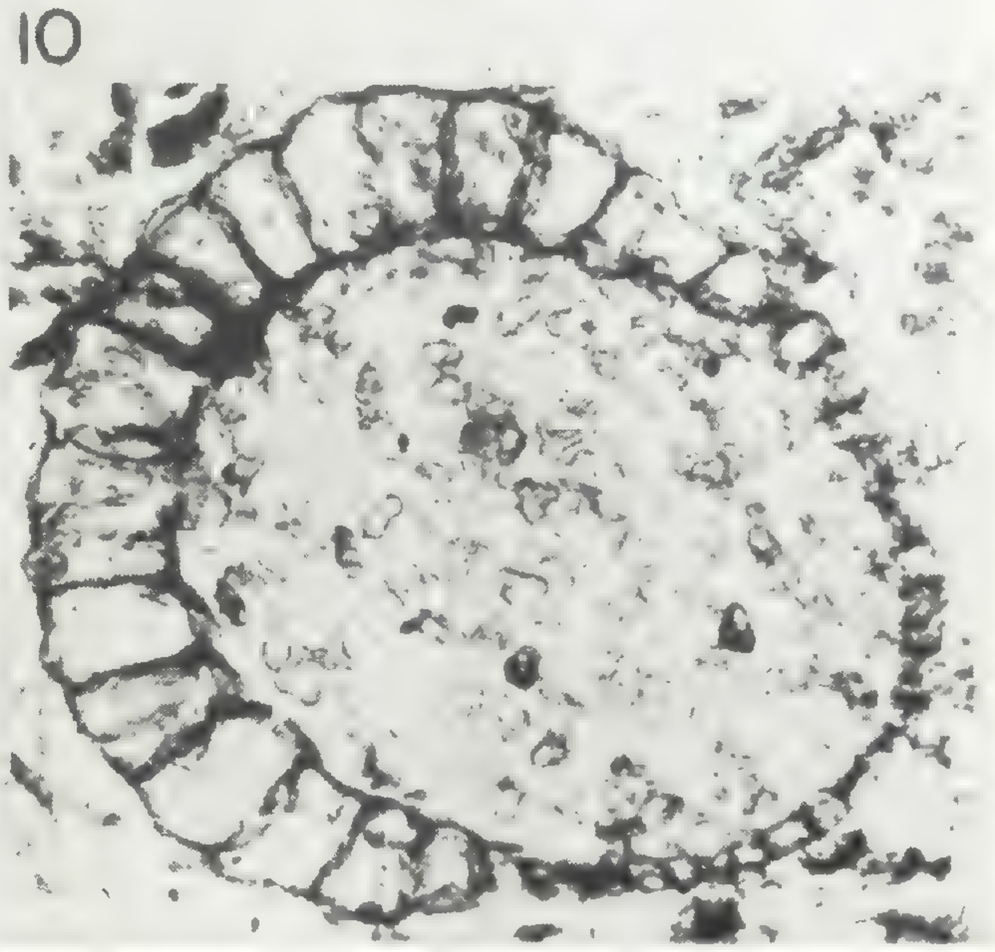
Fig. 9. Spores. Slide #1685, × 1360.

Fig. 10. A single sporangium, sectioned transversely. Note the markedly differential thickening of the sporangial wall, which is a single cell in thickness. Slide #1686, × 165.

Fig. 11. *Ptychocarpus unitus* Brongniart. A single synangium, sectioned transversely. *a*, bundle of receptacle; *b*, its parenchyma; *c*, tapetun; *d*, spores; *e*, *f*, common envelope of synangium. Figure and explanation from Bower, after Renault, ×60.







MAMAY—FERN FRUCTIFICATIONS

Explanation of Plate

PLATE 3

Cyathotrachus altissimus

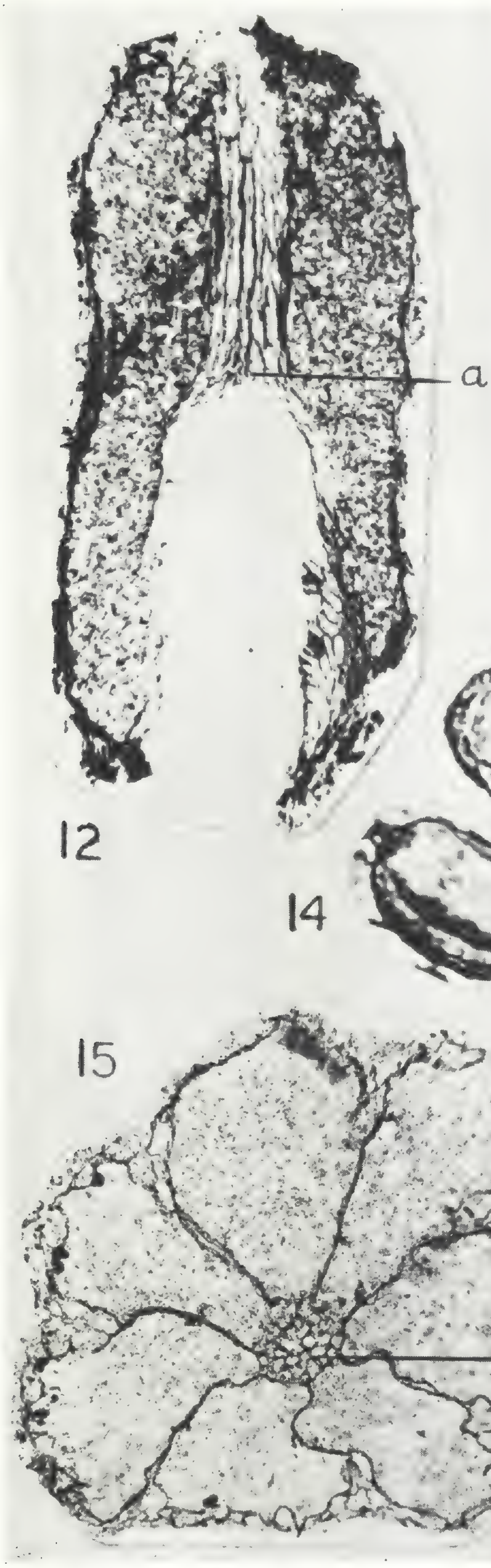
Fig. 12. A single synangium, sectioned longitudinally. Note the hollow cup-like portion of the fructification, extending distally from the termination of the central column (*a*). Slide #1687, × 50.

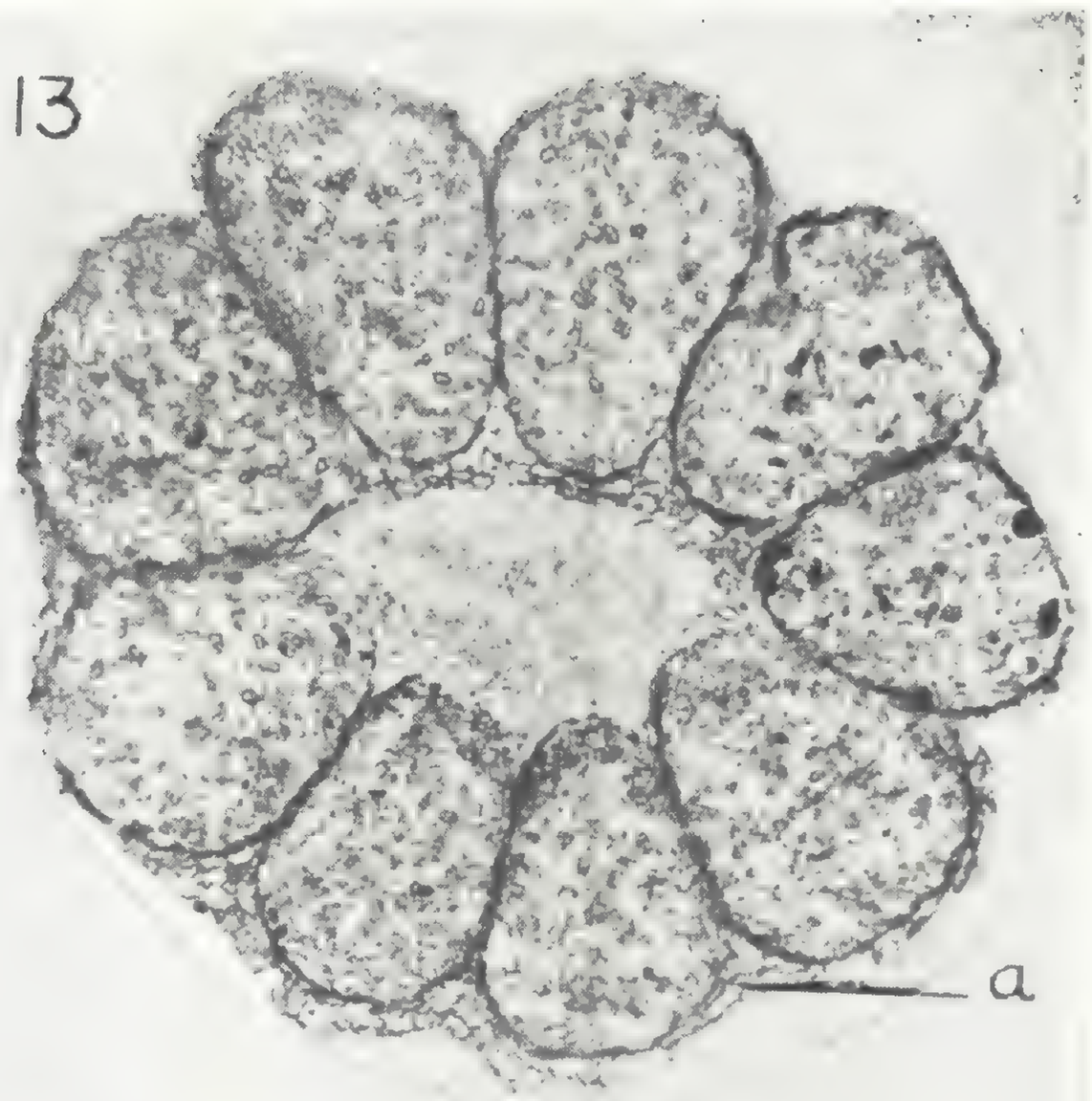
Fig. 13. A single synangium, sectioned transversely through its hollow cup-like portion, with spore masses intact. *a*, continuous synangial wall (compare with *e*, *f*, fig. 11). Slide #1692, × 60.

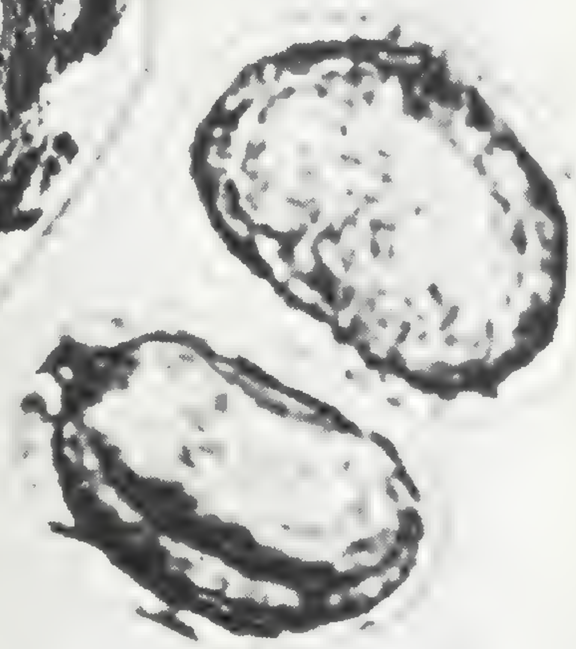
Fig. 14. Spores. Slide #1688, × 1300.

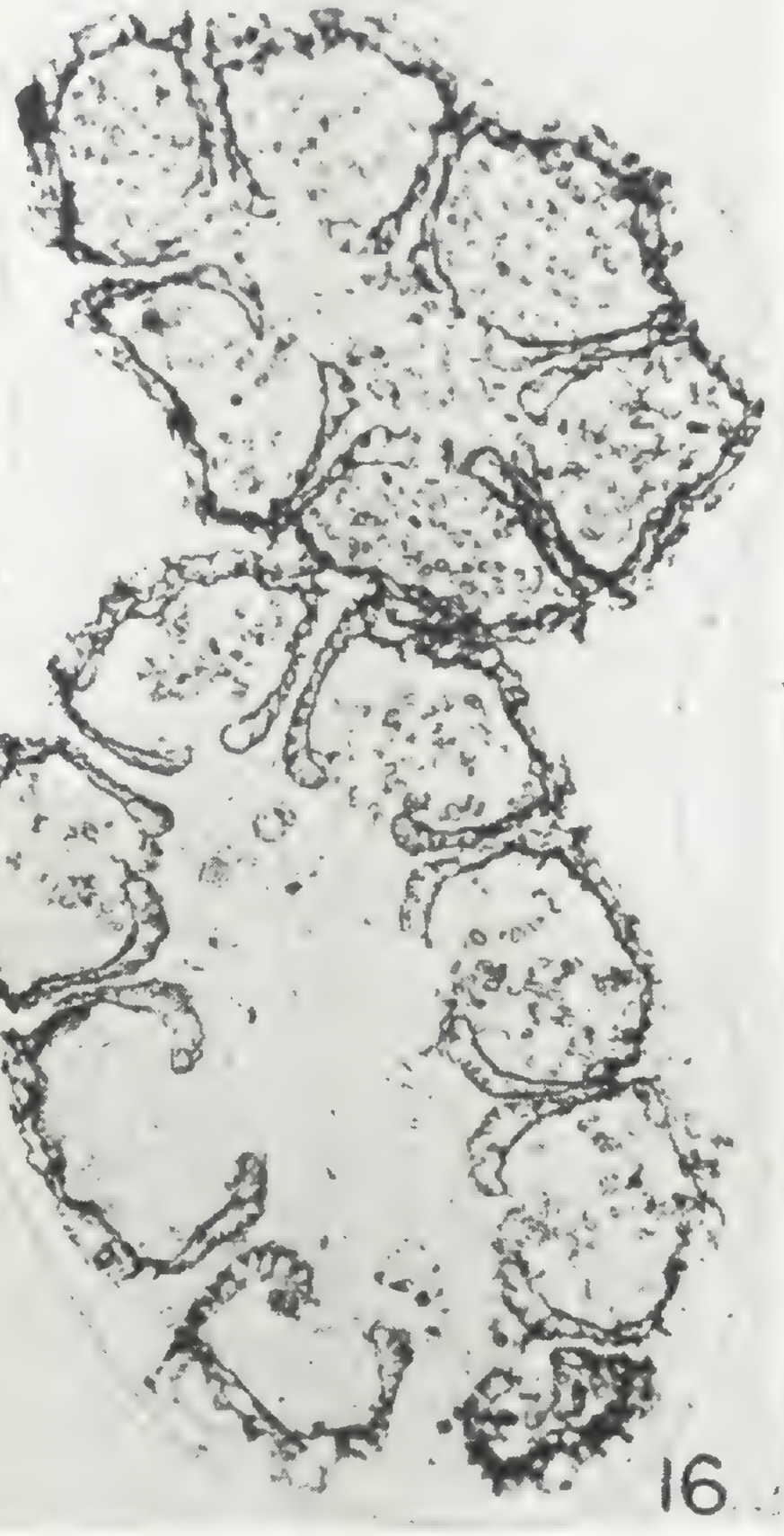
Fig. 15. A single synangium, sectioned transversely through the central column. *a*, central column; *b*, synangial wall. Slide #1688, × 60.

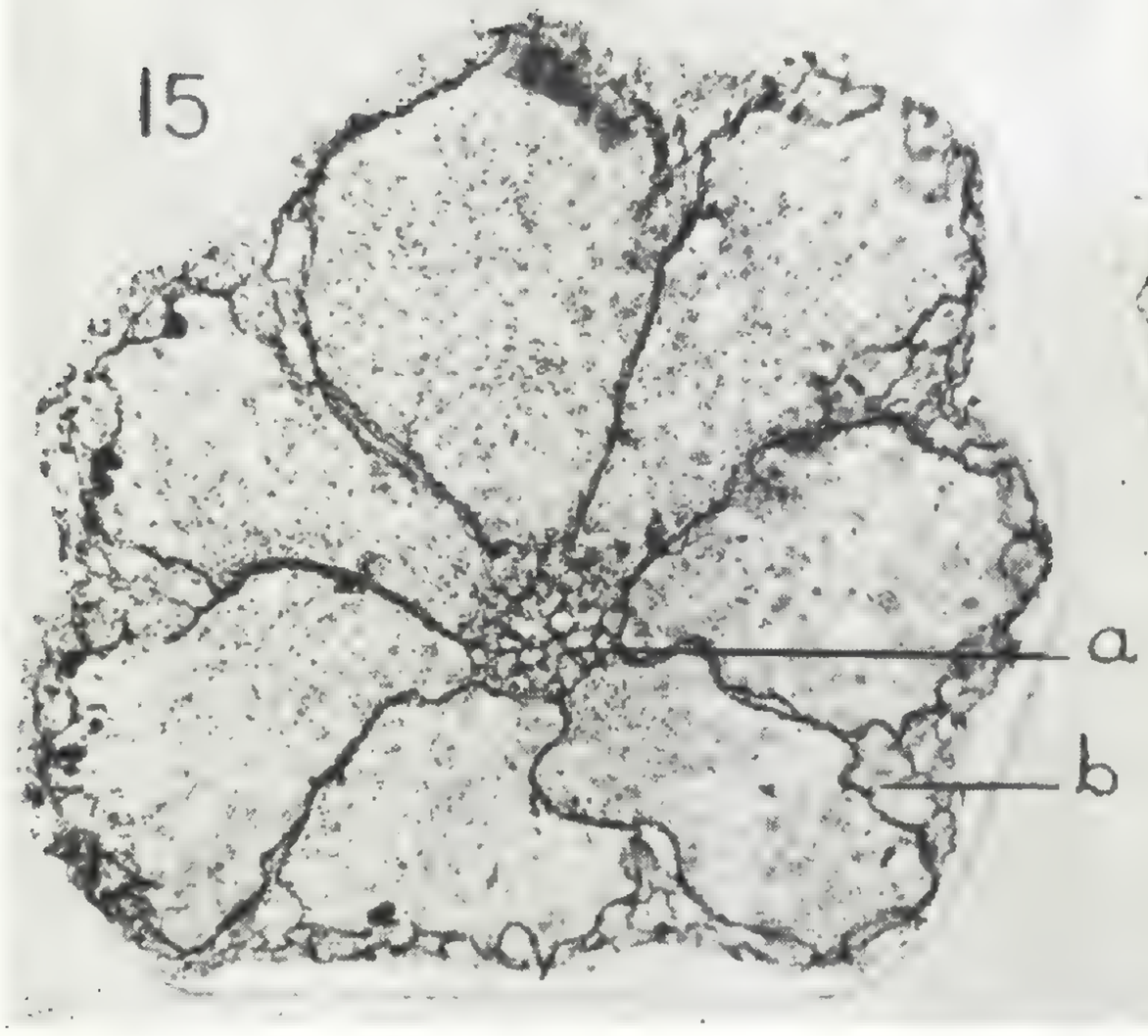
Fig. 16. Two dehiscent synangia, sectioned transversely. Note that the sporangia have separated from each other and display slits of dehiscence at their innermost surfaces. Slide #1688, × 70.











MAMAY—FERN FRUCTIFICATIONS

Explanation of Plate

PLATE 4

Scolecopteris latifolia

Fig. 17. Two pinnules, transversely sectioned, with attached synangia. Note the broad, strongly inflexed margins of the pinnules. Slide #1697, × 15.

Fig. 18. A pinnule sectioned parallel to the plane of the lamina, with several synangia shown sectioned transversely. Note the predominance of trilocular synangia, and the dense black contents of the cells of the epidermis and hypodermis (*a*). Slide #1694, × 18.

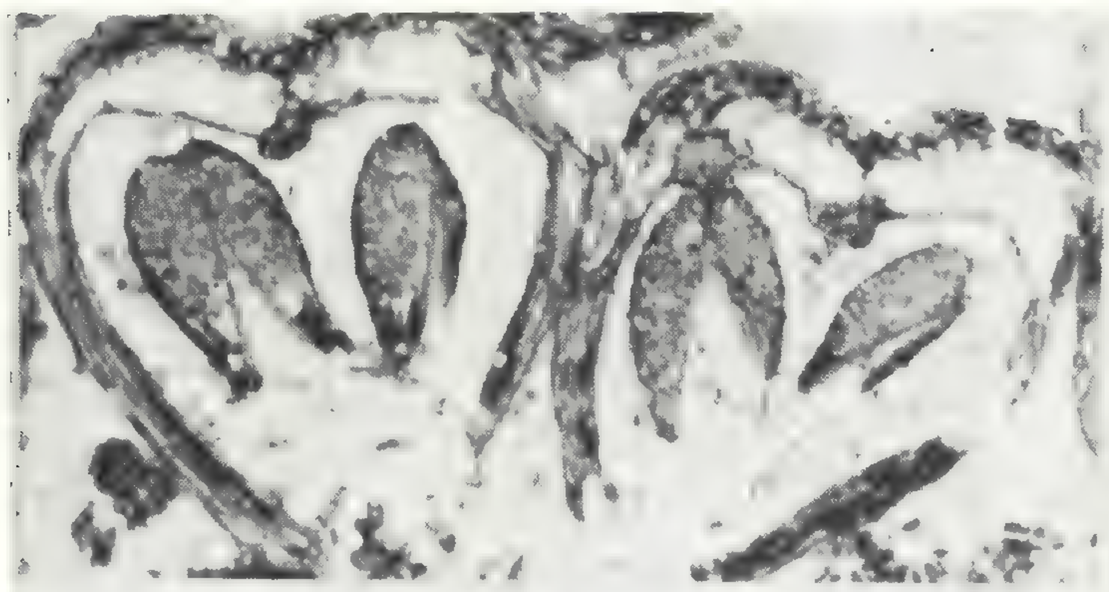
Fig. 19. A single pinnule and portions of the margins of two adjacent ones, sectioned in a plane paralleling that of the lamina, but below the apices of the fructifications. The penultimate midrib is shown at the upper portion of the figure. Note that the inflexed pinnule margins are dissected, appearing as series of separate crescent-shaped bodies with dense cellular contents. *a*, a single lobe of the pinnule margin. Slide #1694, × 16.

Fig. 20. Spore. Slide #1697, × 800.

Fig. 21. A single pinnule, sectioned in a plane parallel to its midrib, but near one "shoulder" of the pinnule, with the section intercepting several of the attached synangia. The penultimate midrib is shown at the left, transversely sectioned. At the bottom of the figure are shown transverse sections of the strongly inflexed marginal lobes, one of which is indicated at point *a*. Slide #1696, × 17.

Fig. 22. Higher magnification of the lobe seen in figure 21, *a*. Note the epidermal hairs and the dense cellular contents. Slide #1696, × 70.

Fig. 23. A single pinnule, sectioned parallel to the plane of the lamina. A portion of the midrib and several of the lateral veins are shown, along with several synangia, sectioned transversely near their bases. The hypodermis appears as a nearly continuous black outline to the pinnule. Slide #1694, × 17.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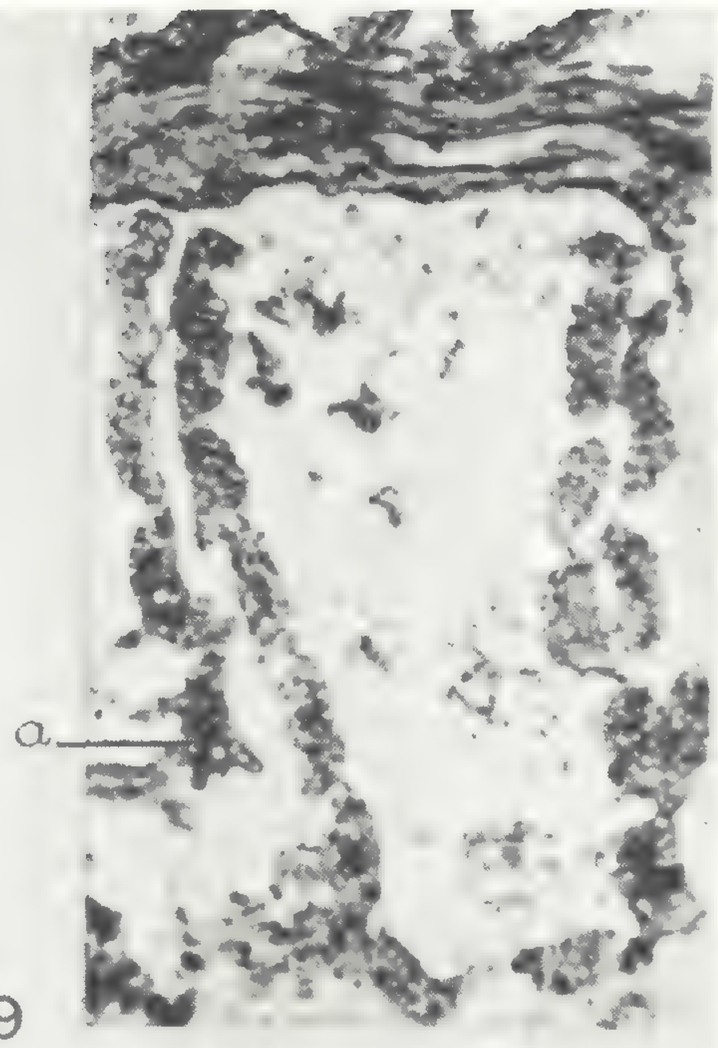

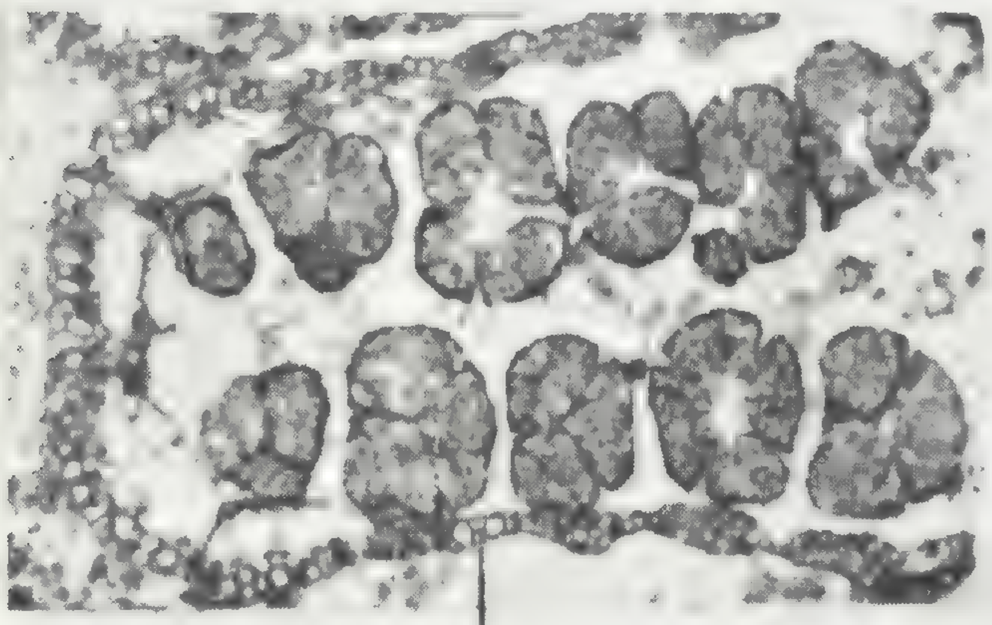

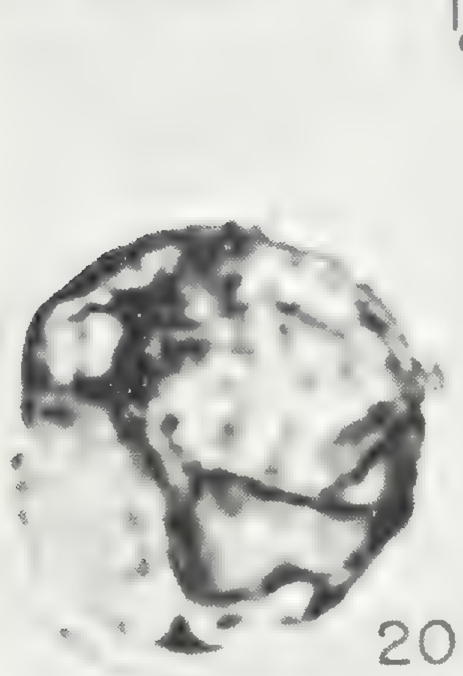
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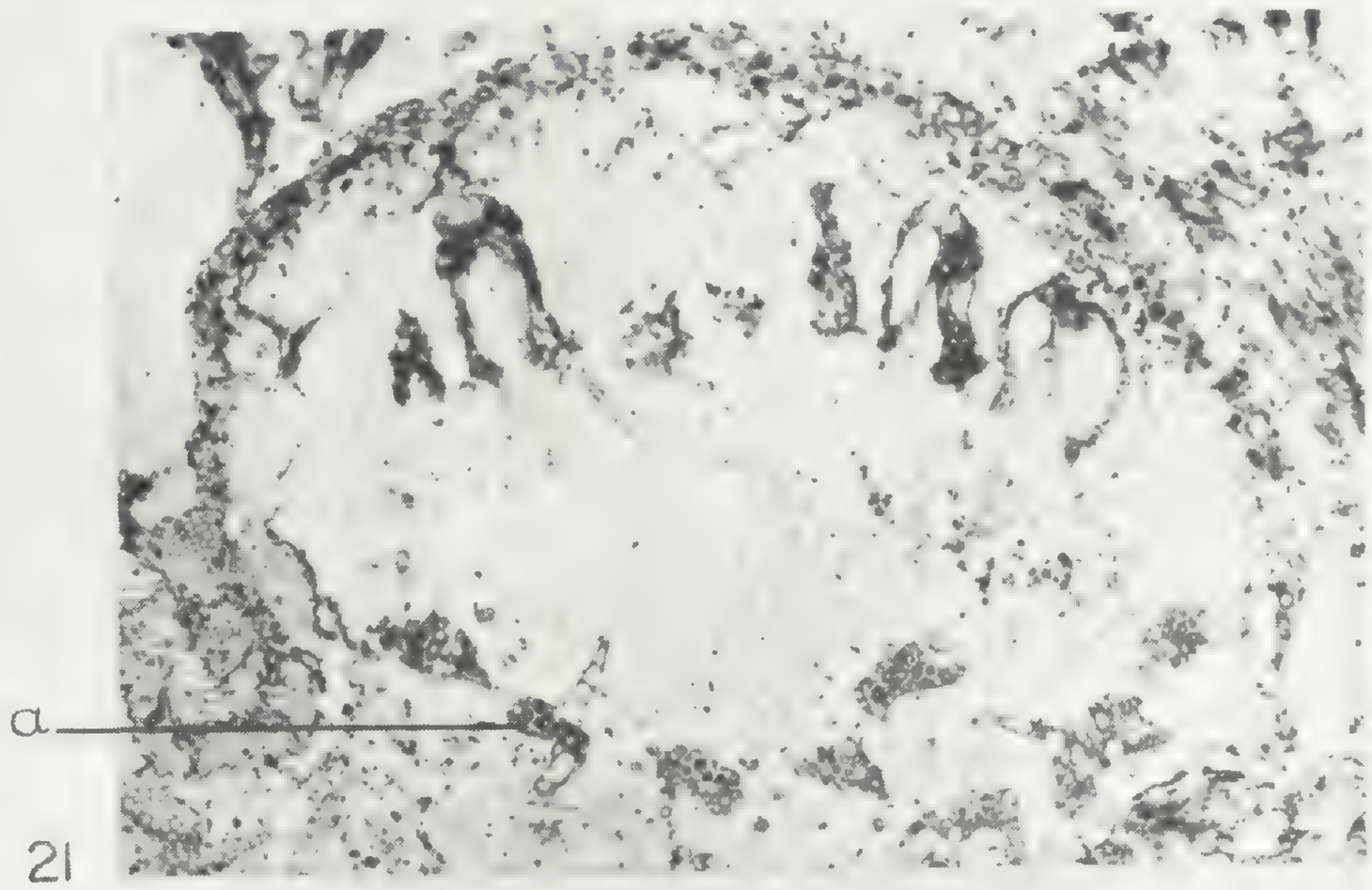

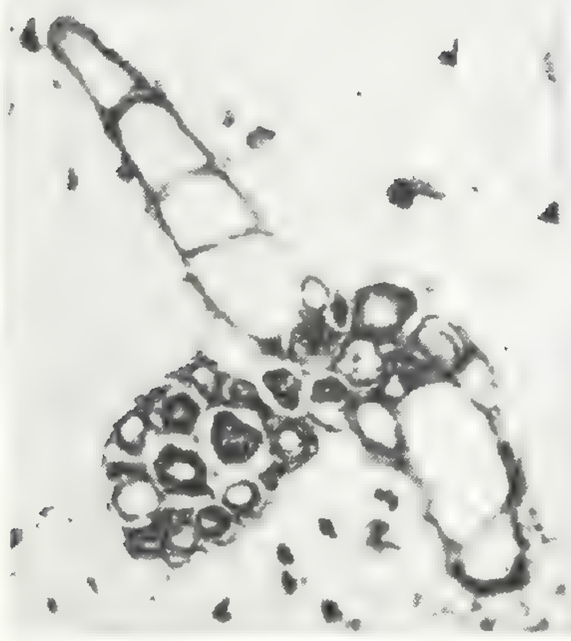
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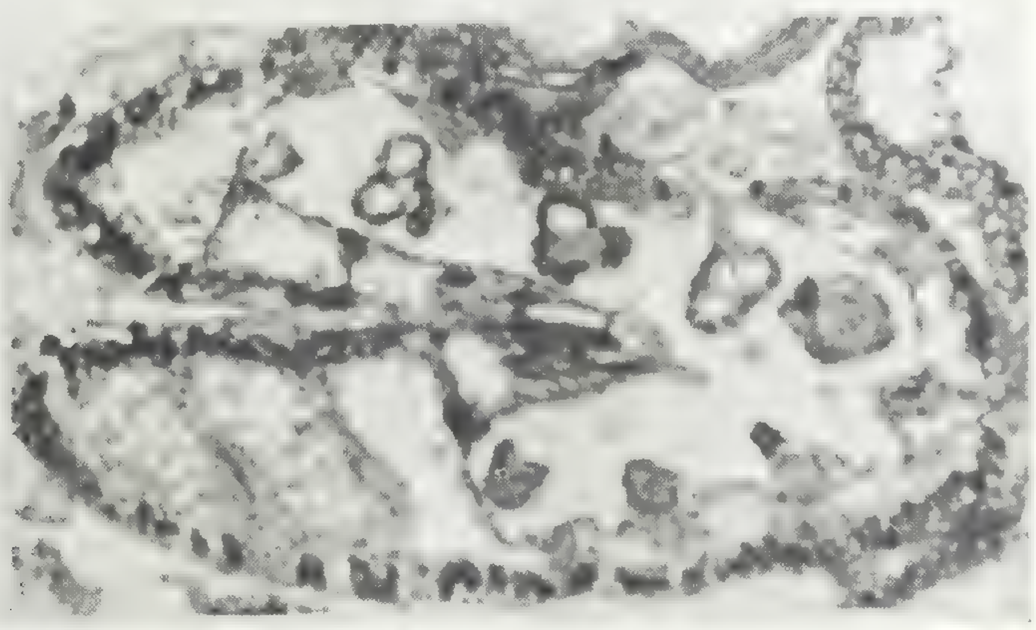
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MAMAY—FERN FRUCTIFICATIONS

Explanation of Plate

PLATE 5

Scolecopteris iowensis

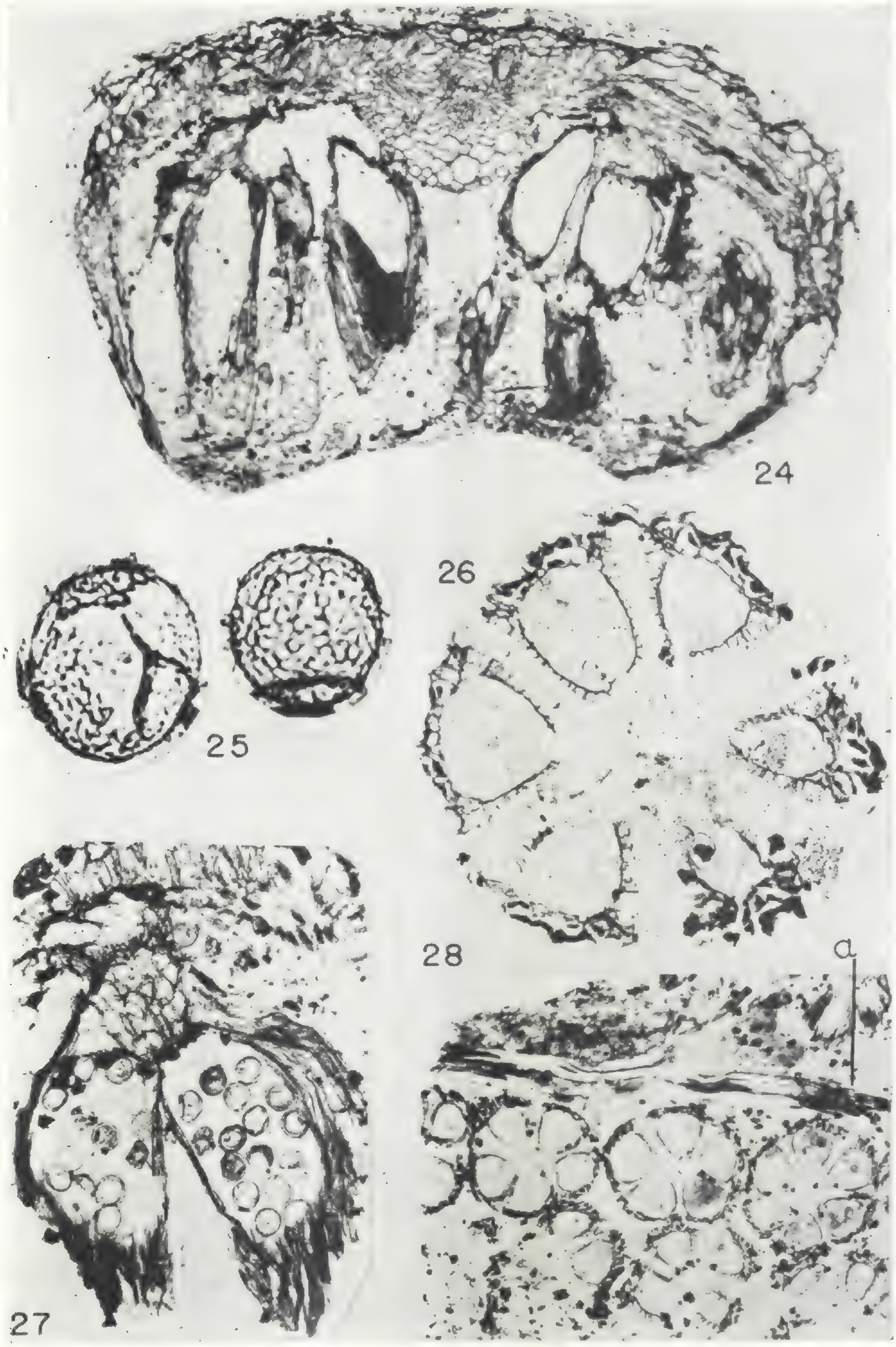
Fig. 24. Transverse section of a pinnule, with fructifications attached. Note the strong midrib and inflexed pinnule margins. Slide #1698, × 36.

Fig. 25. Spores. Note the reticulate exines and triradiate ridge. Slide #1702, × 350.

Fig. 26. Transverse section of a synangium containing six sporangia. Note the dense cellular contents of the outer walls, and the thin inner sporangial walls. Slits of dehiscence are evident at the innermost portion of each sporangial wall. Slide #1702, × 74.

Fig. 27. Longitudinal section of a synangium, showing its pedicellate attachment to the pinnule. Slide #1698, × 60.

Fig. 28. Portion of a pinnule, sectioned in a plane paralleling the lamina. At one side of the midrib (*a*) are shown two closely appressed rows of synangia. Slide #1702, × 20.



MAMAY—FERN FRUCTIFICATIONS

Explanation of Plate

PLATE 6

Scolecopteris minor Hoskins var. *parvifolia* Mamay

Fig. 29. Transverse section of a pinnule with two synangia attached. Note the strong midrib and inflexed pinnule margins. Slide #1704, × 66.

Fig. 30. Spore. Note the triradiate ridge. Slide #1703, × 1650.

Fig. 31. Transverse section of a synangium containing five sporangia. Slide #1708, × 66.

Fig. 32. Pinnule sectioned in a plane paralleling the plane of the lamina. The midrib (*a*) is seen departing from the penultimate midrib (*b*). To the right of the pinnule midrib, several lateral veins are shown; to the left, five synangia are shown in transverse section. Slide #1706, × 20.

Fig. 33. Longitudinal section of a synangium, showing the pedicellate attachment to the lamina. Slide #1708, × 80.

MAMAY—FERN FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 7

Scolecopteris incisifolia

Fig. 34. Portion of a pinnule sectioned in a plane parallel to the midrib and at right angles to the plane of the lamina (this approximates the section shown in diagram C, text-fig. 1). The lamina proper is shown at the upper portion of the figure (*a*); below this are shown four synangia, transversely sectioned (*b*); below the synangia are several of the inflexed lobes of the pinnule margin (*c*). Slide #1709, × 45.

Fig. 35. Two immature synangia, longitudinally sectioned. Note the vascularized pedicels (*a*). Slide #1709, × 55.

Fig. 36. Transverse section of a lobe of the pinnule margin. Slide #1709, × 100.

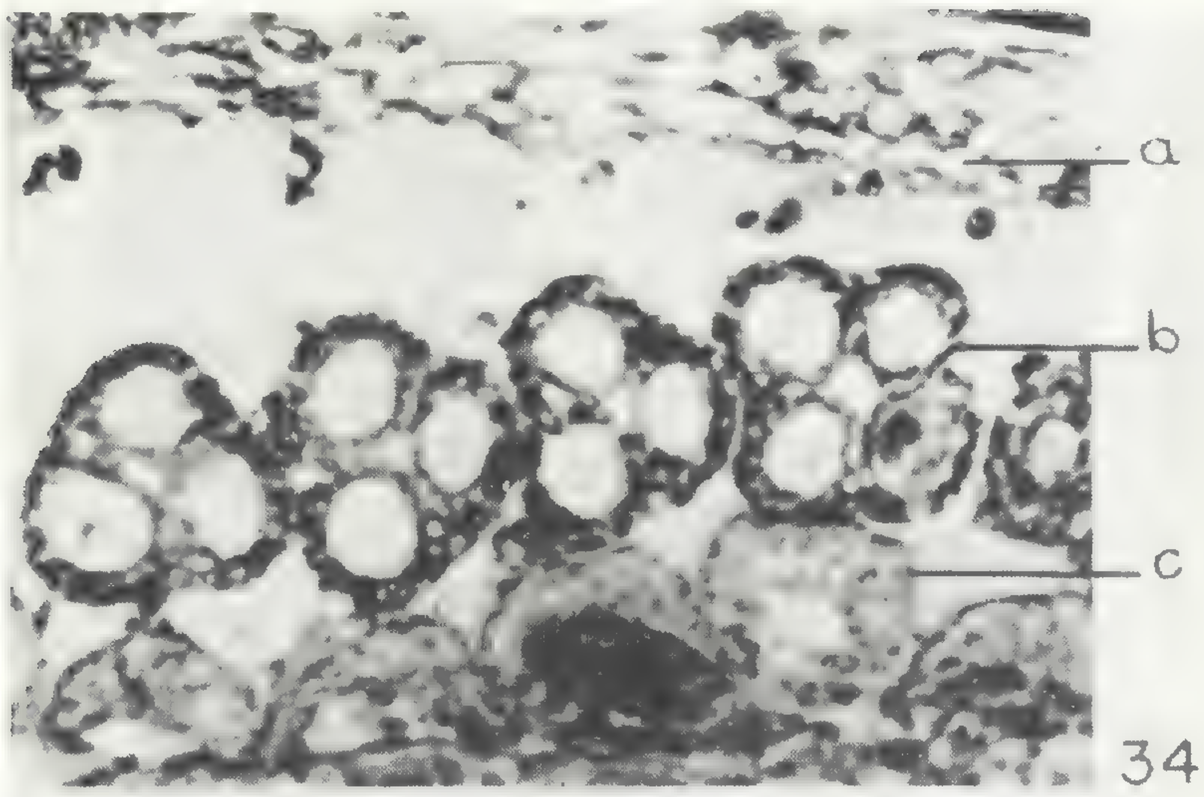
Fig. 37. Pinnule sectioned in a plane parallel to that of the lamina. (For clarification see fig. 38.) Slide #1712, × 18.

Fig. 38. Line drawing of the pinnule section shown in fig. 37. A portion of the midrib is shown at the right. The inflexed pinnule margin at the upper portion of the drawing is shown as a continuous tissue, with portion of a synangium attached (*a*). The opposite margin has been sectioned in a slightly lower plane, and is seen to be dissected. A marginal lobe is shown at point *b*.

Fig. 39. Spores. Note the thick spore walls. Slide #1711, × 1000.

Fig. 40. Longitudinal section of a synangium. Slide #1711, × 75.

Fig. 41. Transverse section of two synangia, each containing four sporangia. *a*, inflexed lobe of pinnule margin. Slide #1711, × 55.



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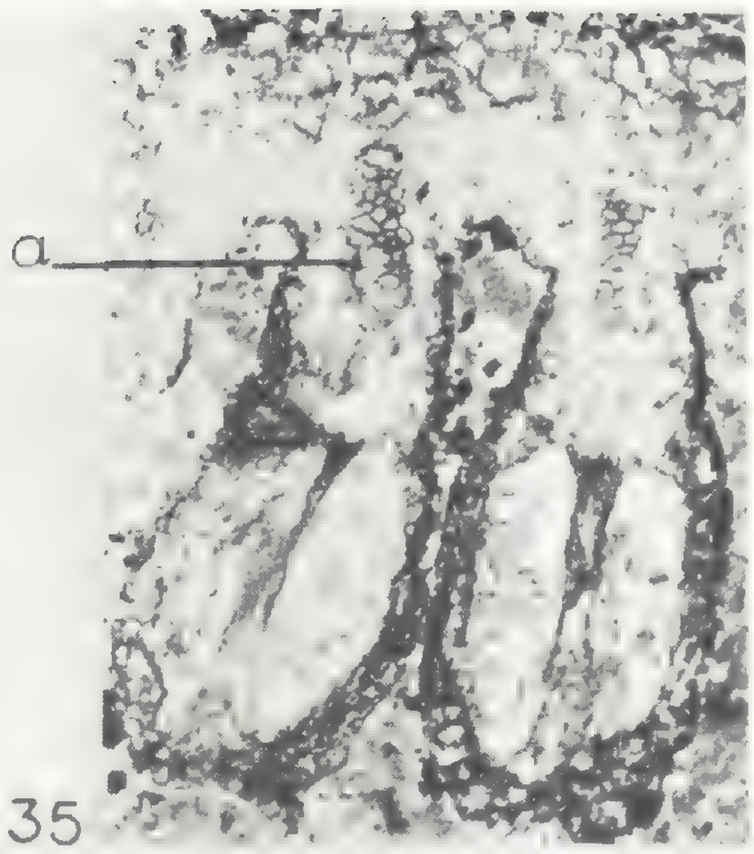

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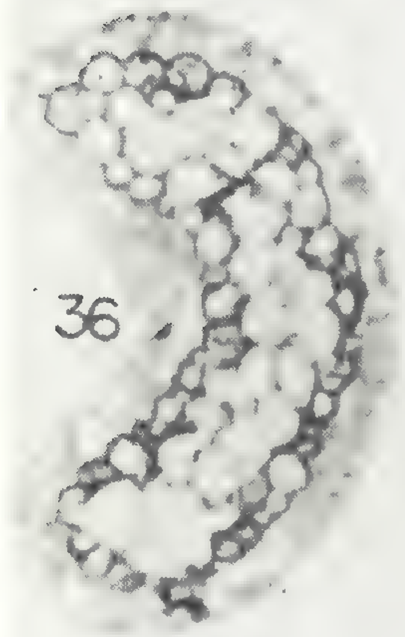

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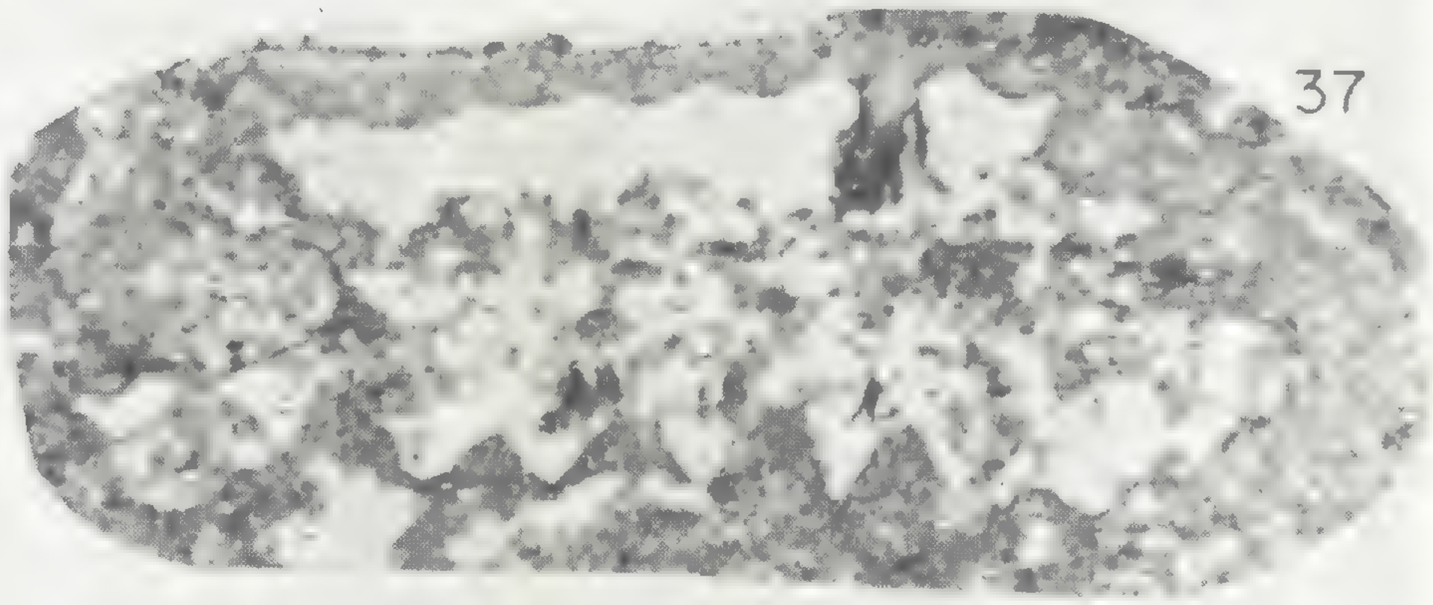

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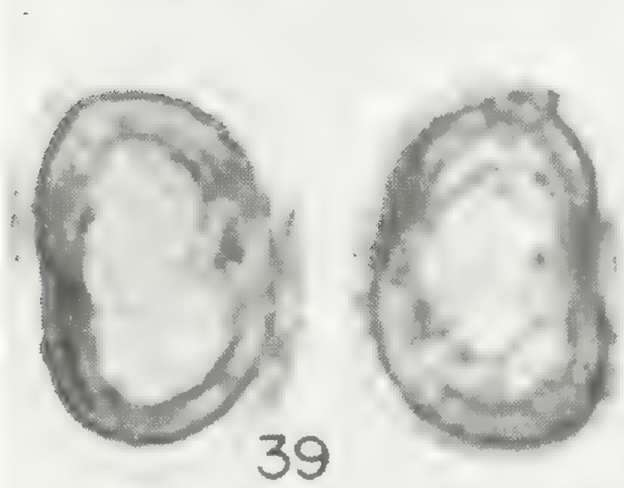

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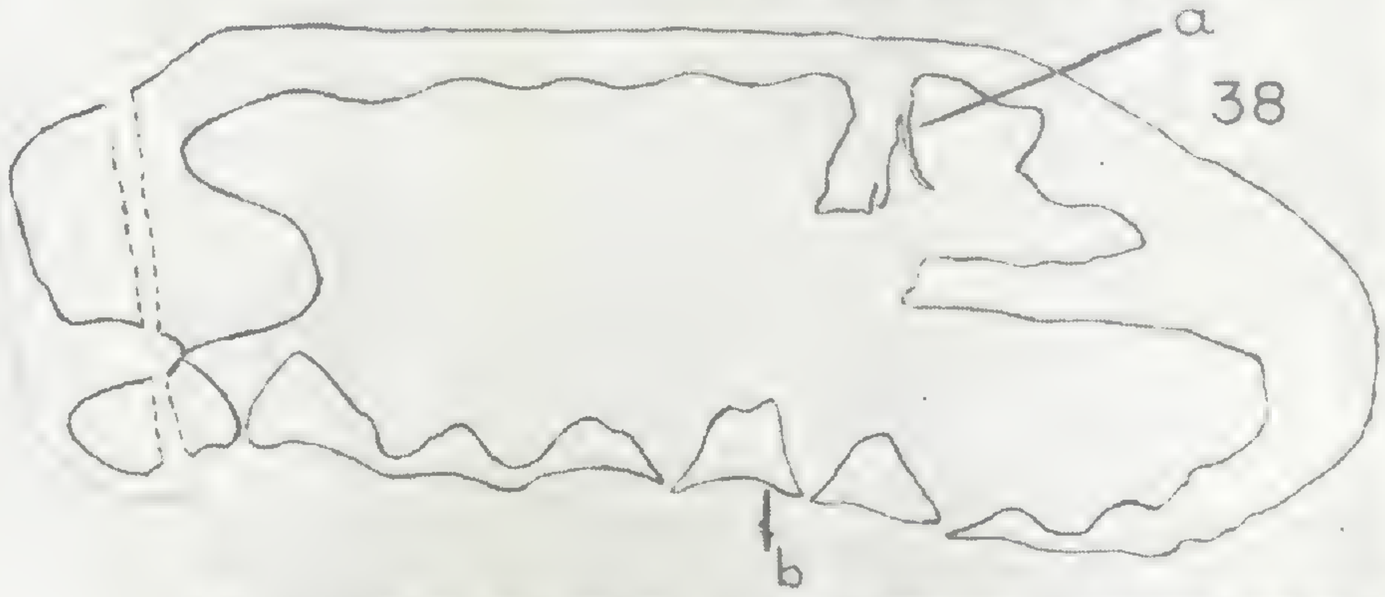

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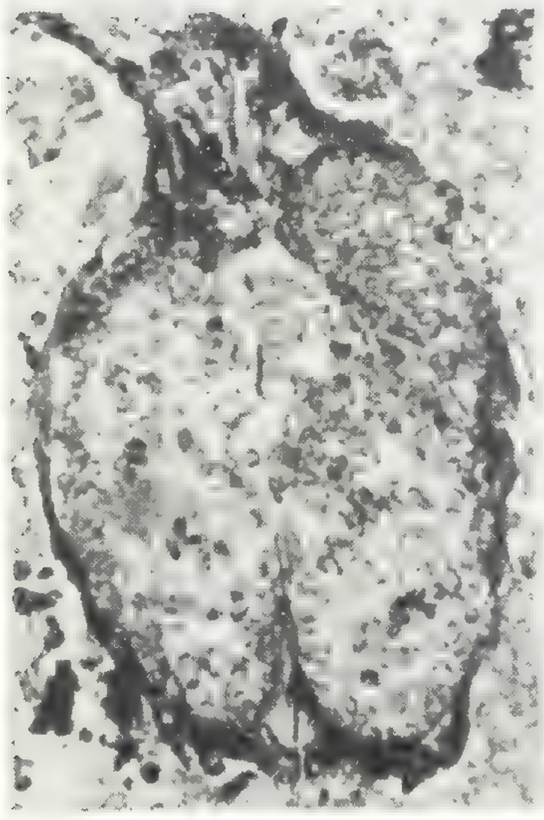

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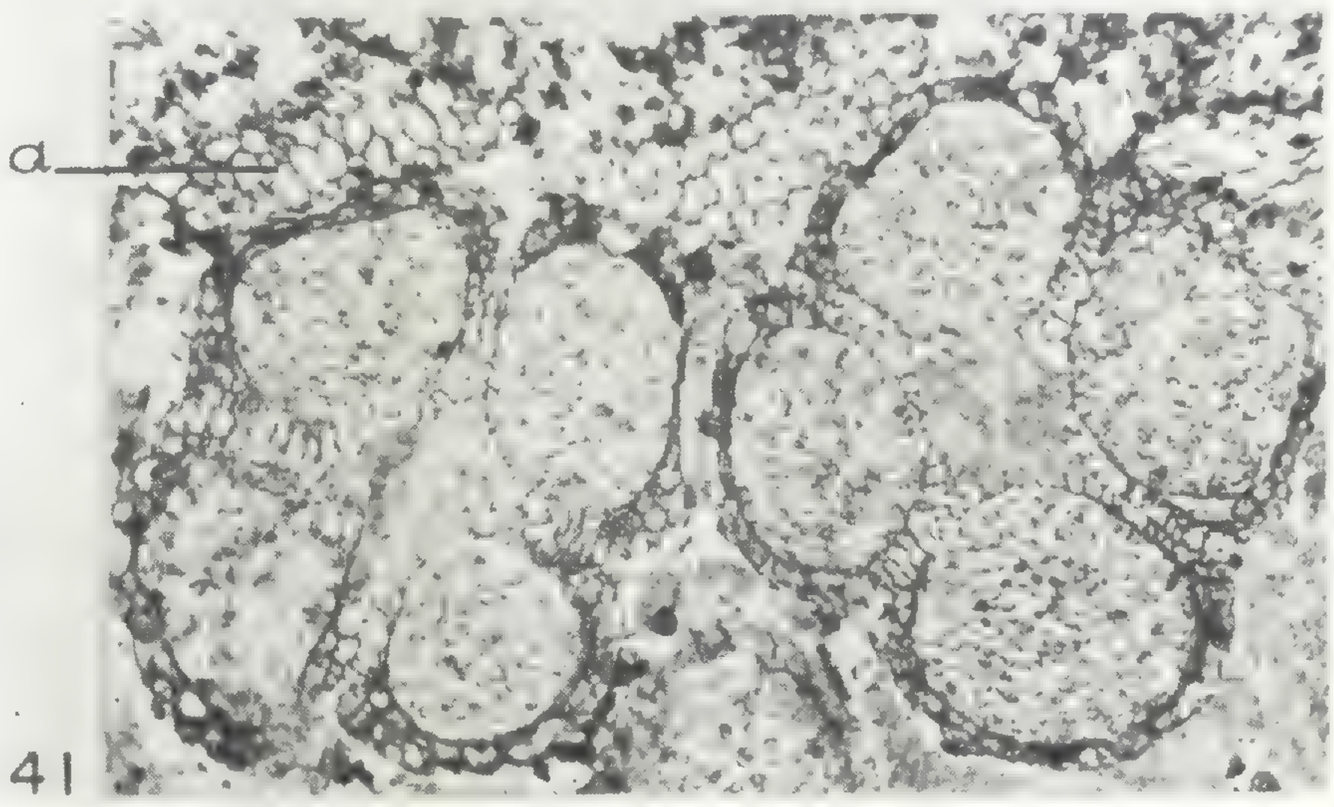

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EXPLANATION OF PLATE

PLATE 8

Scolecopteris major

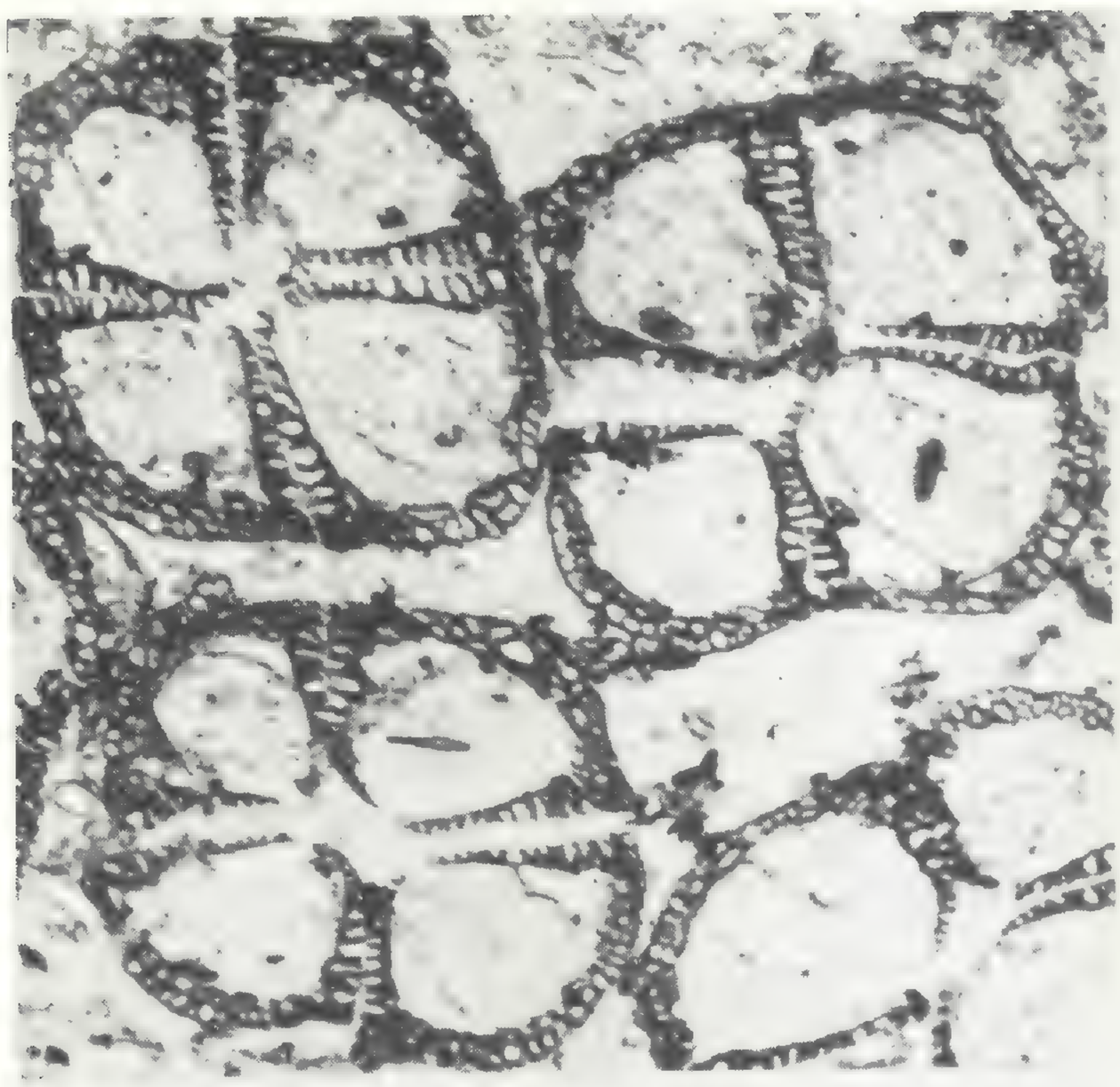
Fig. 42. Transversely sectioned synangia, each containing four sporangia. Note the thick outer walls of the sporangia and the slits of dehiscence along the innermost surfaces of the sporangia. Slide #1717, × 50.

Fig. 43. Longitudinal-transverse section of a synangium. The two sporangia in the upper portion of the figure are shown in transverse section; the two remaining sporangia are shown in a three-dimensional (longitudinal-transverse) view. Slide #1717, × 50.

Fig. 44. Longitudinal section of a synangium. Note the short, thick pedicel. Slide #1714, × 36.

Fig. 45. Spores. Note the thick triradiate ridge. Slide #1713, × 450.

Fig. 46. Apex of a sporangium, showing two multicellular hairs attached. Slide #1715, × 100.



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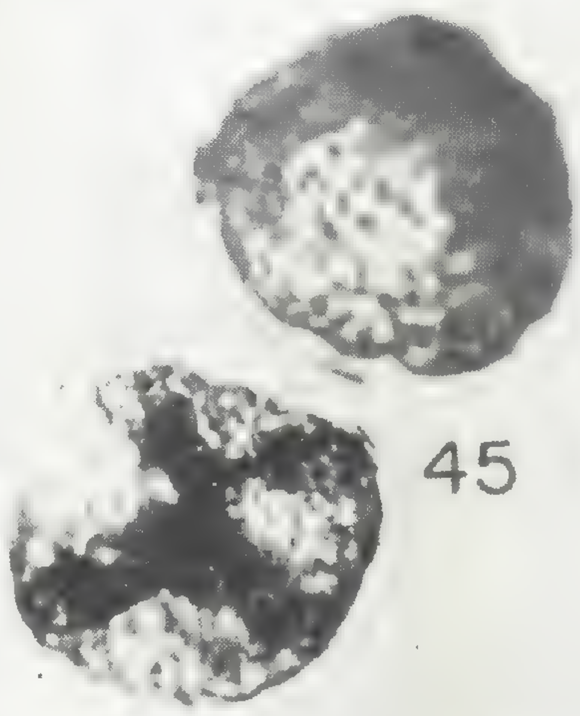

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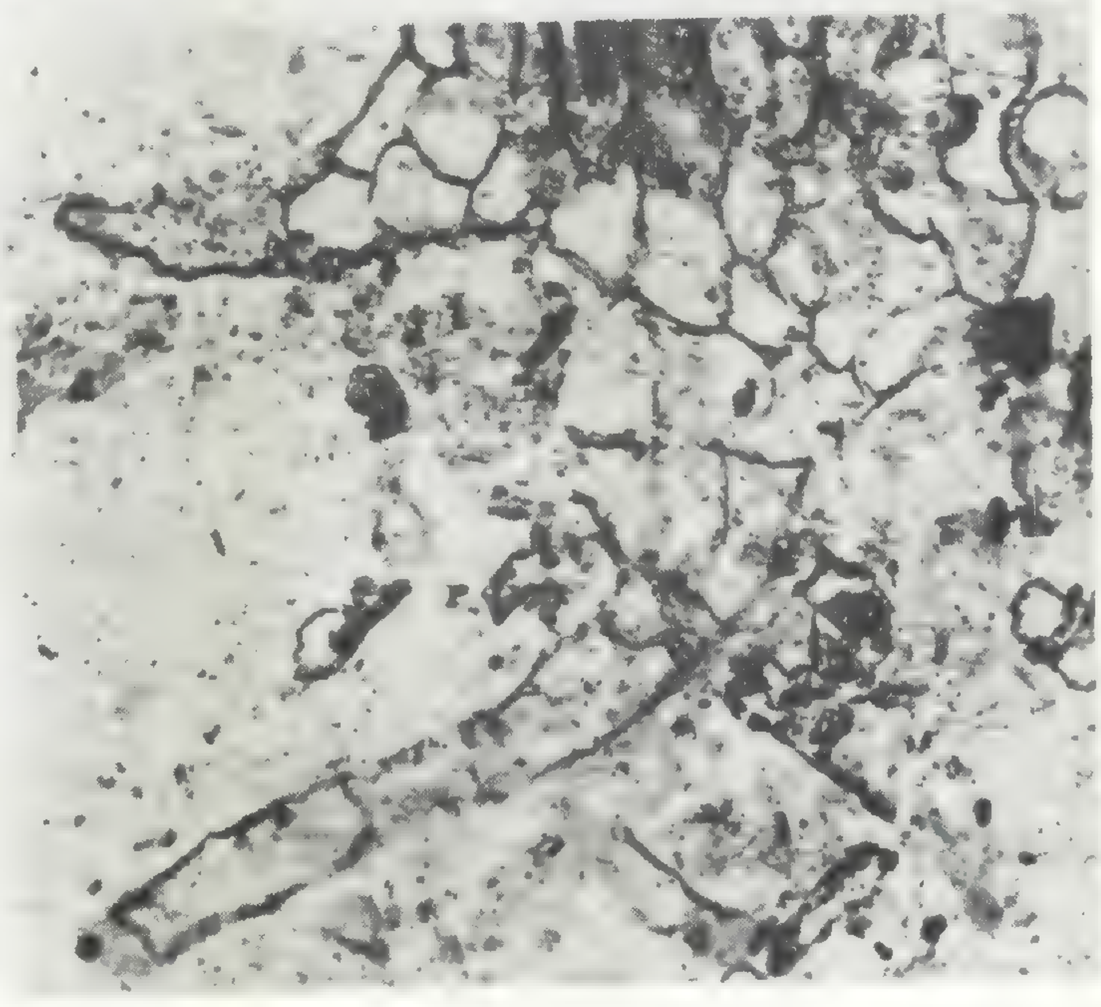

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MAMAY—FERN FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 9

Eoangiopteris Andrewsii

Fig. 47. A pinnule sectioned in a plane parallel to that of the lamina, and slightly below it. The midrib (*a*) and several synangia are shown. Slide #1723, × 20.

Fig. 48. Two synangia. *a*, inflexed pinnule margin; *b*, receptacle of synangium. (For clarification of this section see text-fig. 2, D, which approximates the section shown in fig. 48, represents a section cut through plane *b*-*b'* of diagram B.) Slide #1720, × 54.

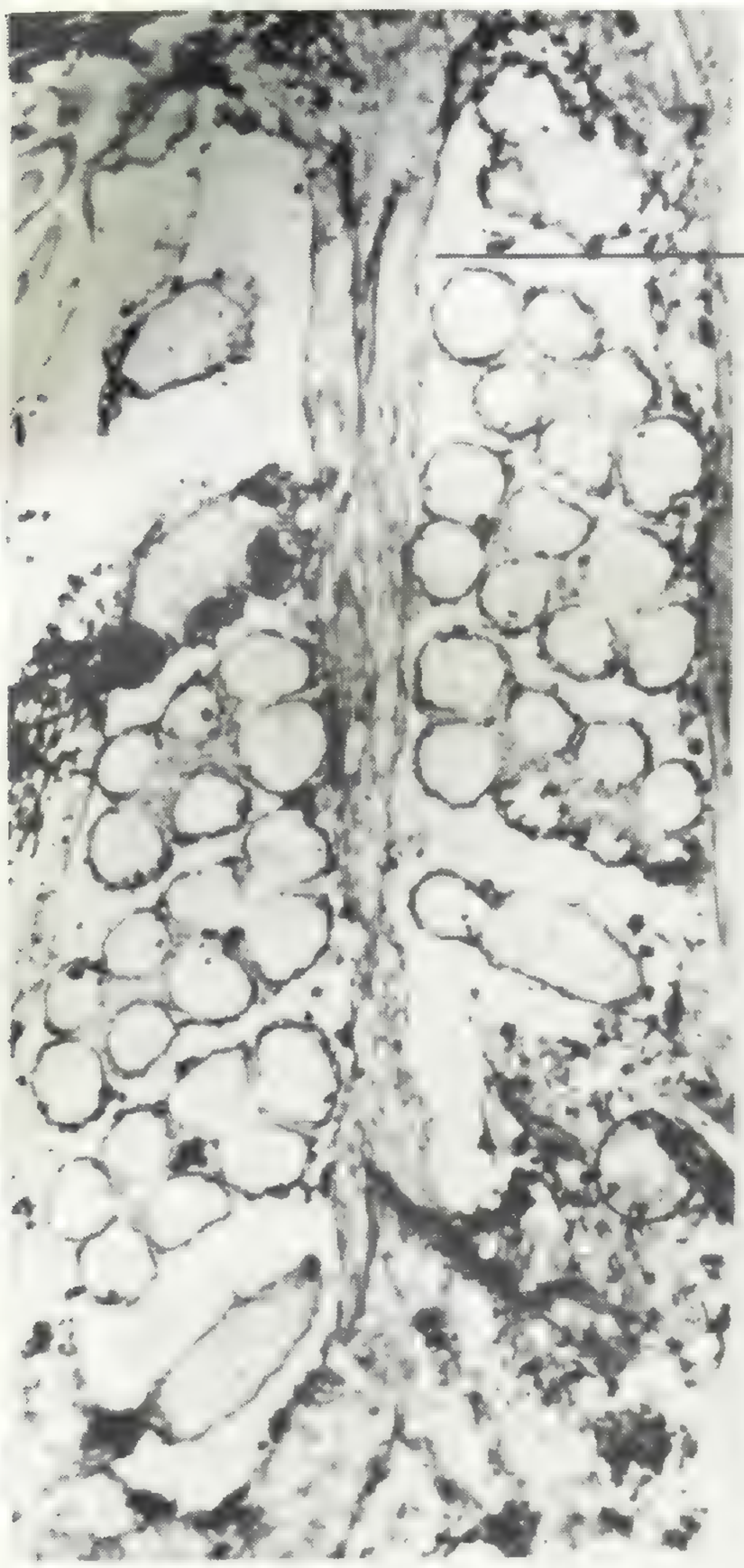
Fig. 49. Transverse section of a synangium. *a*, receptacle. (For clarification of this and fig. 50, see text-fig. 2, C, which represents a section taken through plane *a*-*a'* of B. The receptacle is stippled.) Slide # 1723, × 52.

Fig. 50. Transverse section of a synangium, taken in a plane above the receptacle. Note the slits of dehiscence along the innermost surfaces of the sporangia. Slide #1719, × 53.

Fig. 51. Longitudinal section of synangium. *a*, receptacle. Slide #1722, × 40.

Fig. 52. Spore. Note the reticulate exine. Slide #1719, × 370.

Fig. 53. Transverse section of a pinnule midrib. *a*, u-shaped vascular bundle; *b*, multicellular hair. Slide #1726, × 50.



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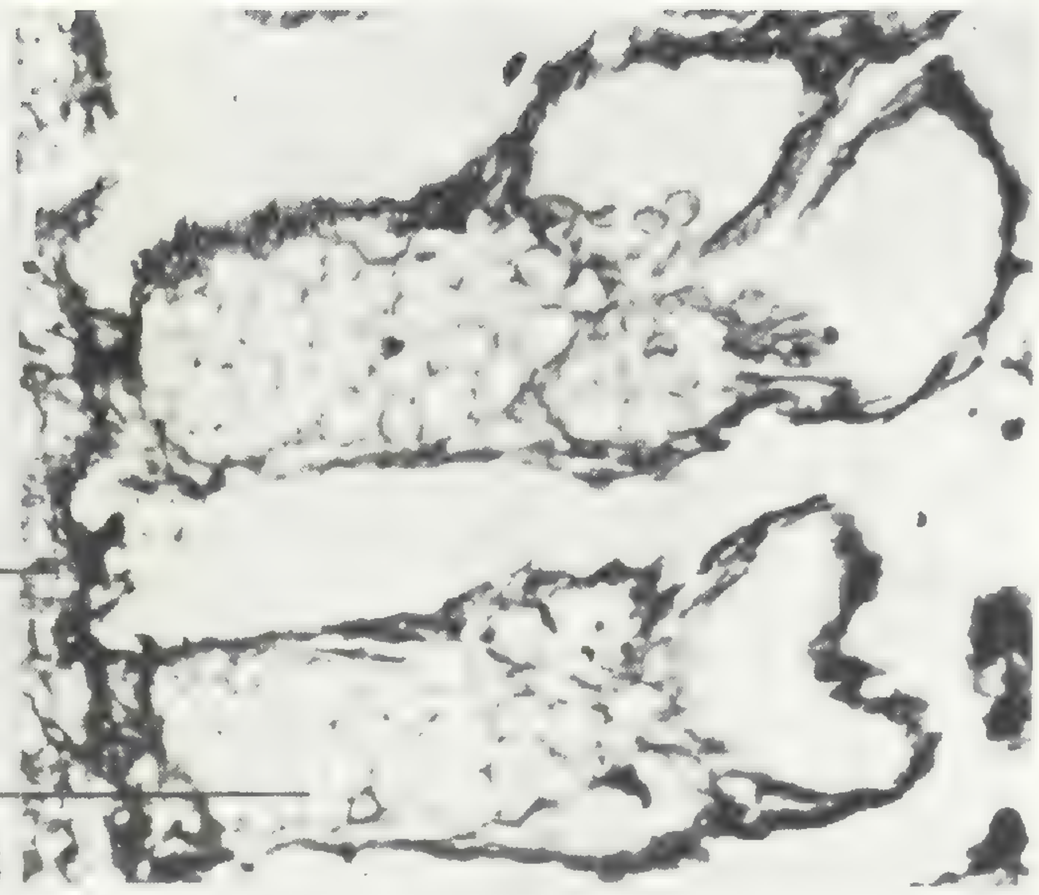

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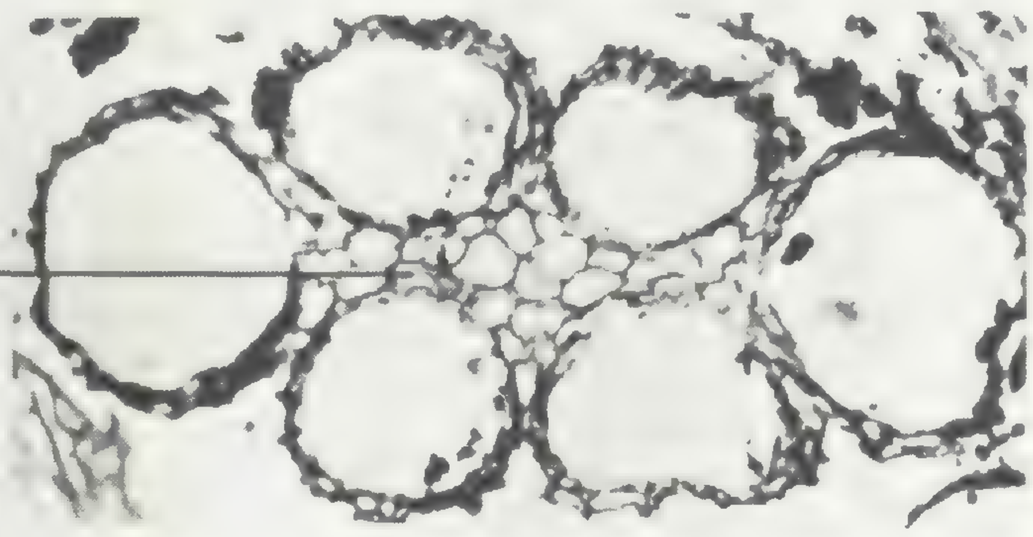

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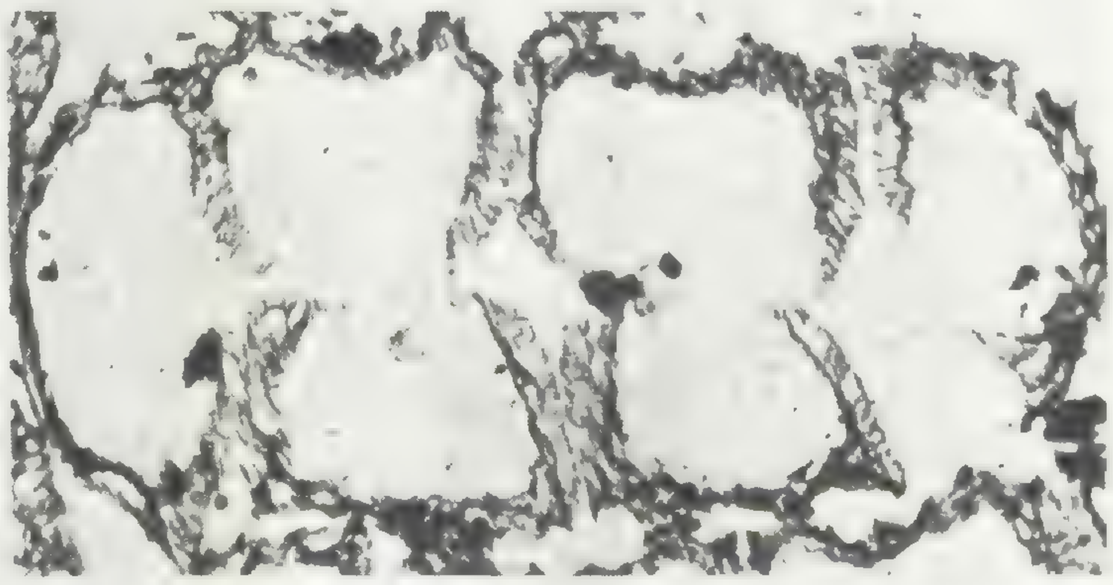

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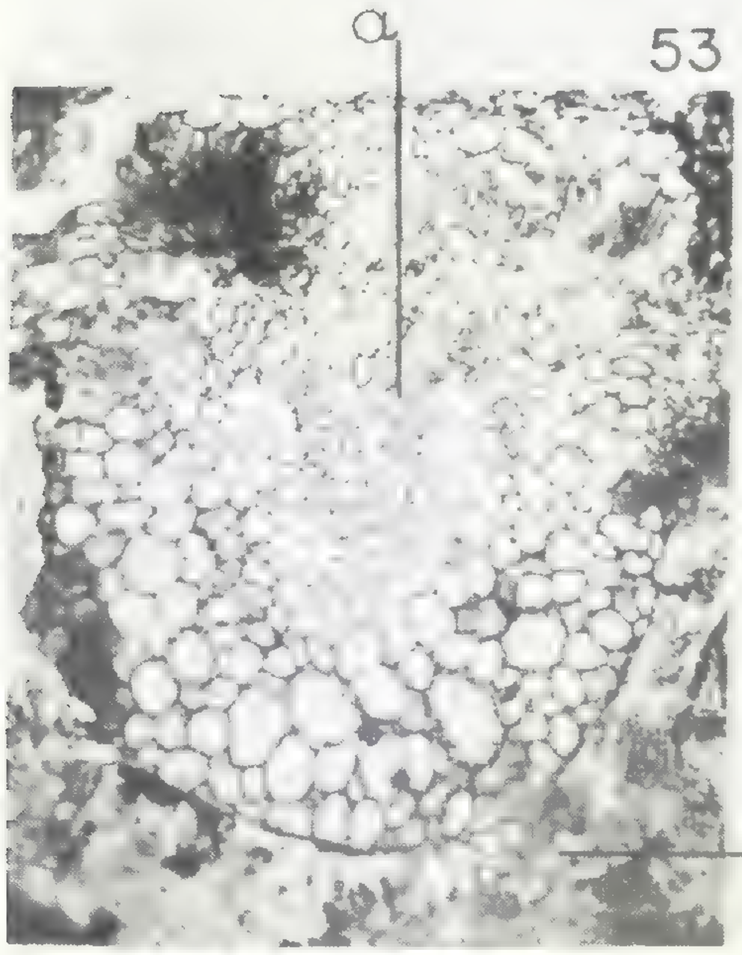

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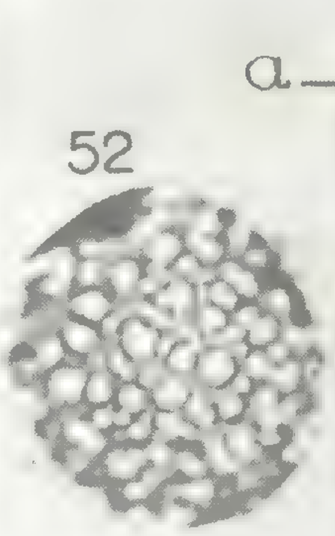

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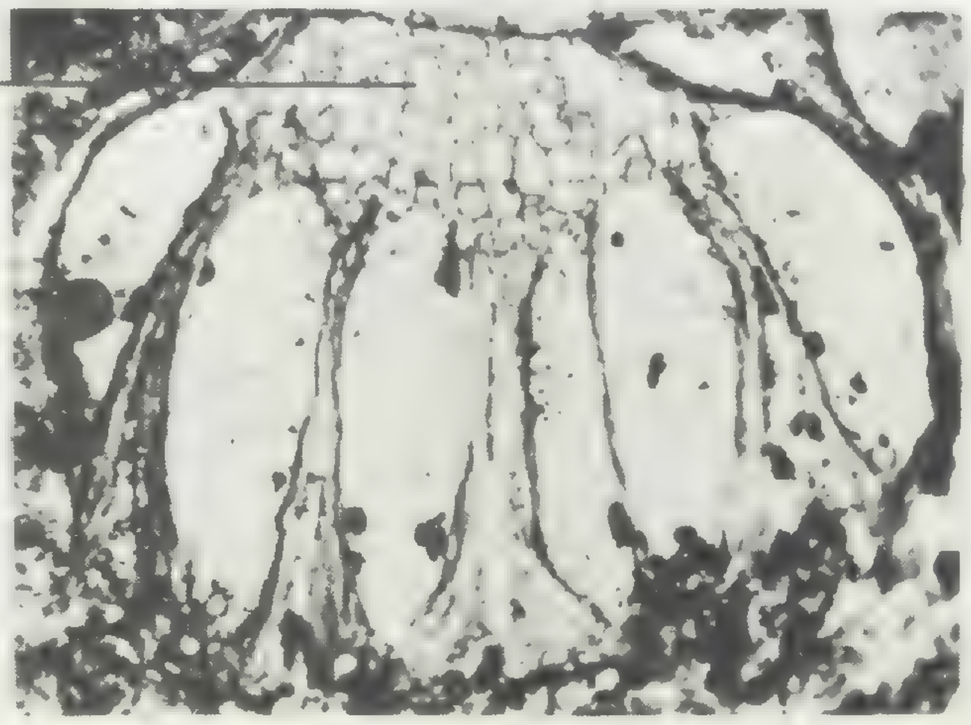

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THE AMERICAN SPECIES OF SARCOSTEMMA R. BR. (ASCLEPIADACEAE)*

RICHARD W. HOLM**

As subjects for monographic study the Asclepiadaceae have been rather generally neglected since the beginnings of taxonomy. This may have been due, in part perhaps, to their minor economic importance and to the impression that genera in the family are easy neither to define nor to determine. A more important factor, however, has been the prevalent opinion that the flowers are so complex morphologically as to render the plants very difficult to study. One cannot deny with candor that these points are well-taken, but the result has been that no satisfactory general account of the family exists, making identification extremely arduous. Many ill-correlated small genera have been described because of their presumed uniqueness; and the vast potential of absorbing morphologic and ecologic topics in this interesting group has not been appreciated.

I was led to consider the Asclepiadaceae because of my interest in their adaptations for insect pollination and the bearing which this has on their phylogeny. It is remarkable that the pattern of evolution and the taxonomic difficulties encountered in this family and in the Orchidaceae are very similar. Except for certain differences which will be discussed below, these two families, the most specialized for insect pollination in Dicotyledones and Monocotyledones respectively, show similar developments in floral structure, aggregation of the pollen into pollinia, and a bewildering array of forms which almost defy classification. In many respects, however, the Asclepiadaceae are much the more specialized with regard to structure of the pollinium and the method of pollination. And their floral evolution, though to a certain extent parallel with that of the orchids, has been along slightly different lines. For example, the Asclepiadaceae are constructed upon a basic pattern of actinomorphy, in contrast to the strongly zygomorphic orchids. To what

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extent can we attribute these similarities and differences to the intimate relationship between the plants and their insect pollinators?

It soon became apparent that a study of these subjects can only be based on a dependable taxonomic system and a clear understanding of the morphology of the structures involved. With these points in mind, an investigation of *Sarcostemma* was undertaken as an introduction to the complexities of tropical American Asclepiadaceae. Not without a thorough review of all the genera, however, can the ideals of a sound morphology and taxonomy be realized, and it is not suggested that this account of one genus is more than an introduction to a program that would require years of study to complete.

Sarcostemma probably has been the least neglected of the genera in its alliance, for the plants are attractive both scientifically and esthetically. In the New World, the species are vines with umbelliform or racemiform inflorescences of fragrant, showy flowers. The flower, with the waxy corona bladders in the center, somewhat resembles that of the wax plant, *Hoya*, in those species with rotate corollas. The species of the group formerly assigned to *Philibertia*, which have campanulate flowers, were often cultivated in English greenhouses of the past century. And still fairly common in collections of succulents are the leafless African and Asian species, which occasionally produce clusters of yellow or green flowers.

In this paper, the New World species of *Sarcostemma* have been studied monographically; and, in order to maintain perspective, the Old World forms are treated synoptically. Unfortunately, the paucity of specimens and the general nomenclatural confusion of the Eastern Hemisphere species make it impossible to gain any understanding of their relationships, or even to estimate the number of species involved. It is possible that the evolutionary development of these species of the drier parts of the tropical and subtropical regions of the Old World has been along different lines from that of the New World forms. At any rate, many rather obscure genera are confused in the literature, and also, the misapplication of such names as *viminale* and *aphyllum* for leafless plants, throughout most of the Old World floristic accounts, has created a situation of extreme taxonomic chaos. A number of leafless species of *Euphorbia* have been confused with the sarcostemmas so that it is by no means easy to decide which family is being discussed in a given treatment.

With the detailed knowledge of the American species in mind, I have begun a reinvestigation of the morphology of the flower in the tribe Asclepiadeae. The results of such a study can be used as a basis for a classification of genera and species enabling one to view them as a whole and helping to remove that impression of chaos which has discouraged so many.

HISTORY OF THE GENUS

I do not propose to record in detail the history of the various species which have been attributed to *Sarcostemma* and its segregates. It seems desirable, however, to chronicle briefly those genera which have been related nomenclaturally. In order

to understand the taxonomic history of *Sarcostemma*, it is essential to recognize that there are two main problems involved. First, there is the misapplication of several generic names and the consequent confusion in their usage up to the present day. Second, there is the question of how many segregates can be maintained without endangering the integrity of the genus as a practical unit.

Sarcostemma was described by Robert Brown[1] in 1809 in his classic paper on the separation of the Apocynaceae and Asclepiadaceae. The only species known to him at that time were succulent lianas of Asia and Africa having the leaves reduced to scales. They were characterized by rotate flowers provided with a pronounced faucal annulus or outer corona, and an inner corona consisting of five separate, inflated lobes (to which the name alludes). Ten years later, Kunth[2] described, as species of *Sarcostemma*, a series of American forms of similar floral structure, but with laminate leaves. For a species having the corolla campanulate, he inaugurated the new genus *Philibertia* HBK. He also noted that the outer corona in *Philibertia* was less prominent than in *Sarcostemma*.

In his account of the Asclepiadaceae for the 'Prodromus' of De Candolle, Decaisne[3] recognized only the genus *Sarcostemma*, which consisted, however, of two sections: EUSARCOSTEMMA and PHILIBERTIA. The former included both New World and Old World forms with rotate corollas, while the latter contained only New World species with "*corolla urceolato-rotata.*" Decaisne himself described most of the American species of both EUSARCOSTEMMA and PHILIBERTIA included in his account.

The peculiar confusion in the taxonomy of the genus began in 1876 when Bentham[4] referred all of the New World species to the genus *Philibertia* HBK., regardless of the shape of the corolla. Shortly thereafter, Gray[5] and Hemsley[6] made the necessary new combinations for species of the United States and Latin America. Fournier[7], on the other hand, in the 'Flora Brasiliensis', followed Decaisne in the use of *Sarcostemma* for rotate-flowered species, although he had to deal with no species of *Philibertia* (*sensu* HBK.).

In the preparation of his treatment of the Asclepiadaceae for Martius' great work, Fournier apparently made a careful study of the Latin American species. It is interesting to note that a tendency to draw taxonomic lines rather finely was emphasized in his establishment of the genera *Funastrum*[8] and *Cystostemma*[9]. Of the two species included within *Funastrum* by Fournier, only one is referable to *Sarcostemma*, this being *F. angustissimum* (Anderss.) Fourn. of the Galapagos Islands. The other is an Argentine species of *Cynanchum (Ditassa)*. *Cystostemma* was erected for a species which completely lacks the faucal annulus or ring of the corona; in all other respects it is so close to the other New World sarcostemmas

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[1] R. Brown, in Mem. Wern. Soc. 1:50. 1809.
[2] Kunth, in HBK. Nov. Gen. et Sp. Pl. 3:195. 1819.
[3] Decaisne, in DC. Prodr. 8:537. 1844.
[4] Bentham, in Benth. & Hook. Gen. Pl. 2:733. 1876.
[5] Gray, in Proc. Amer. Acad. 12:64–65. 1877.
[6] Hemsley, in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:320. 1881.
[7] Fournier, in Mart. Fl. Brasil. 6^4:233–235. 1885.
[8] Fournier, in Ann. Sci. Nat. Bot. VI, 14:388. 1882.
[9] Fournier, in Mart. loc. cit. 204. 1885.

that nearly all subsequent authorities are in agreement as to its conjunction with that group of species. Both *Funastrum angustissimum* (Anderss.) Fourn. and *Cystostemma umbellatum* Fourn. are here made the bases for monotypic series of subg. CERAMANTHUS.

The most recent treatment of Asclepiadaceae as a whole is that of K. Schumann[10] in 'Die Natürlichen Pflanzenfamilien'. The rather generally unsatisfactory aspects of his system are well-exemplified by his handling of the *Sarcostemma* problem. The American species with campanulate flowers were transferred to the Old World genus *Oxystelma* R. Br., leaving in *Philibertia* only those forms with rotate corollas, while *Sarcostemma* was limited to the Old World forms with scale-like leaves. *Oxystelma* and *Philibertia* were placed in the same subtribe (GLOSSONEMATINAE), while *Sarcostemma* and the synonymous genus *Funastrum* were put into different subtribes (CYNANCHINAE and ASCLEPIADINAE, respectively).

Realizing that the species then included in *Philibertia* did not accord with the original description of the genus, Miss Vail[11] proposed for them the new name *Philibertella*. She concurred with Schumann in the disposition of the campanulate-flowered species. However well-meant her intentions, the name only added to the confusion, for it took its place with *Sarcostemma*, *Philibertia*, and *Oxystelma*, all being used for the same species.

The Swedish asclepiadologist Malme[12] also attempted to rectify the error of Schumann by elevating the subgenus CERAMANTHUS Kunze[13] to the rank of genus. But he cited as synonyms, *Funastrum*, *Cystostemma*, and *Philibertella*. It is difficult to understand why Malme chose *Ceramanthus* when several names of generic rank were available; moreover, the name is antedated by *Ceramanthus* Hassk.[14] and *Keramanthus* Hook. f.[15] Fortunately it never was used as widely as were the other current names.

Schlechter[16], in a critical discussion published in 1915, came to the conclusion that the group of rotate-flowered species of the New World was sufficiently distinct to be designated as a genus and he made the requisite combinations in *Funastrum*. At the same time he reinstated *Philibertia* for the campanulate-flowered species.

Most recently, Woodson[17] has returned to the system of Decaisne, uniting *Funastrum* and *Philibertia* with the Old World forms under the name *Sarcostemma*. Redintegration appears to be the only satisfactory way of solving the problem, for the three groups of species are very close, and characters formerly used to separate them are found to break down when all of the species are studied together. It is the course followed in this paper, where the three groups of species constitute sub-

[10] Schumann, in Engl. & Prantl, Natür. Pflanzenfam. 4^2:189–306. 1895.
[11] Vail, in Bull. Torr. Bot. Club 24:305–311. 1897.
[12] Malme, in Arkiv Bot. 4^{14}:2. 1905.
[13] Kunze, in Linnaea 20:26. 1847.
[14] Hasskarl, in Cat. Hort. Bogor. Alt. 240. 1844.
[15] Hooker f. in Curt. Bot. Mag. *t. 6271*. 1876.
[16] Schlechter, in Fedde's Repert. 13:279–287. 1915.
[17] Woodson, in Ann. Mo. Bot. Gard. 28:193–244. 1941.

genera: EUSARCOSTEMMA, CERAMANTHUS, and OXYSTELMA. When once this step is taken, however, a serious question of generic limits arises. If *Sarcostemma* is to be defined as a stable entity, a number of closely related genera must be placed in synonymy.

As even Schumann realized, the Old World *Oxystelma* R. Br.[18] is very close to *Philibertia* HBK., agreeing in such points as the campanulate corolla and the ring of the corona adnate to the corolla-tube. *Oxystelma* is here reduced to the rank of a subgenus of *Sarcostemma*, and it includes the species formerly assigned to *Philibertia*.

The genus *Pergularia* L.,[19] of Africa and Asia, superficially appears similar to *Sarcostemma* in that the corona consists of five inflated lobes and a porrect ring which is free from the corolla. There are numerous points of difference, however, which I summarize in the following table:

Sarcostemma	*Pergularia*
Corolla rotate-subcampanulate, salverform with an inconspicuous tube, or campanulate	Corolla salverform with a conspicuous tube.
Ring of the corona thick and short, entire.	Ring of the corona thin and relatively long, 5-lobed, and denticulate.
Vesicles of the corona obtuse to acute, very rarely attenuate, never spurred.	Vesicles of the corona long and attenuate, spurred.
Pollinium-sac essentially uniformly fertile, the corpusculum radially compressed.	Pollinium-sac with a narrow, hyaline, outer margin, the corpusculum strongly compressed tangentially.
Follicles glabrous to pubescent.	Follicles rather copiously puberulent, usually echinate.

In view of these differences, especially of the pollinium, it would seem best to maintain *Pergularia* as a separate genus. Decidedly it does not seem advisable to complicate further the synonymy of the sarcostemmas by changing them all to *Pergularia*.

There are a number of other genera which have been put into the synonymy of *Philibertia* HBK. and *Funastrum* Fourn., and these must now be regarded as synonymous with *Sarcostemma*. Such are *Pentagonium* Schauer[20] and *Zosima* Philippi[21], monotypic genera, both of which apply to species of the subgenus OXYSTELMA; the latter is a later homonym of *Zosima* Hoffm.[22]. Similarly, *Lugonia* Wedd.[23] was described on the basis of an Andean plant which represents nothing more than an alpine modification, and which is referred also to subg. OXYSTELMA.

Rather perplexing are *Pentacyphus* Schltr.[24] and the very similar *Tetraphysa*

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[18] R. Brown, in Mem. Wern. Soc. 1:40. 1809.
[19] Linn. Mantissa, p. 8. 1767 (not of other authors), cf. N. E. Brown in Kew Bull. 1907:323, who shows that *Doemia* R. Br. is the same as the Linnean *Pergularia*.
[20] Schauer, in Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1:364. 1843.
[21] Philippi, Sert. Mend. Alt. 29. 1871.
[22] Hoffman, Gen. Umbell. 145, *t. 4*. 1814.
[23] Weddell, Chloris Andina 2:49. 1857.
[24] Schlechter, in Engl. Bot. Jahrb. 37:605. 1906.

Schltr.[25] While they diverge considerably from *Sarcostemma* as exemplified by the type species, the former is sufficiently close to species of subg. OXYSTELMA to be considered a separate section of subg. OXYSTELMA, and *Tetraphysa* inevitably follows it.

The following synopsis, then, summarizes the structure of the genus as I view it; and in it I take the opportunity to describe a new section and to make several nomenclatural adjustments for Old World forms which will not be discussed further taxonomically.

- Subg. CERAMANTHUS
  - Ser. PANNOSA — *S. pannosum*
  - Ser. CLAUSA — *S. glaucum*, *S. clausum*
  - Ser. CYNANCHOIDES — *S. bilobum*, *S. odoratum*, *S. gracile*, *S. crispum*, *S. elegans*, *S. Torreyi*, *S. cynanchoides*, *S. hirtellum*, *S. arenarium*
  - Ser. ANGUSTISSIMA — *S. angustissimum*
  - Ser. FLAVA — *S. flavum*
- Subg. OXYSTELMA
  - Sect. PHILIBERTIA — *S. campanulatum*, *S. Gilliesii*, *S. albiflorum*, *S. solanoides*, *S. stipitatum*, *S. lysimachioides*
  - Sect. PENTACYPHUS — *S. andinum*, *S. Lehmannii*
  - Sect. EUOXYSTELMA[26] — *S. esculentum*[27]
- Subg. EUSARCOSTEMMA[28] — (several species)

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[25] Schlechter, loc. cit. 616. 1906.

[26] **Euoxystelma** R. Holm, sect. nov.: coronae squamae ovoidae apice caudatae incurvatae gynostegium superantes, coronae annulus et columna pubescentes; caudiculae obsoletae. T.: *Sarcostemma esculentum* (L.f.) R. Holm.

[27] SARCOSTEMMA **esculentum** (L.f.) R. Holm, comb. nov. *Periploca esculenta* L.f. Suppl. 168. 1781.

[28] Subg. **Eusarcostemma** (Decne.) R. Holm, stat. nov. Sect. *Eusarcostemma* Decne. in DC. Prodr. 8:538. 1844.

Morphology

All the species of *Sarcostemma* are suffrutescent, dextrorsely twining or trailing vines. In the tropics they may climb high into trees and shrubs, but in alpine or desert areas they are reduced to semi-erect or prostrate subshrubs, variously woody or succulent.

The primary root generally is slightly thickened, forming a slender tap-root. Aerial adventitious roots have been noted in several plants which had been growing in very moist habitats; apparently they are never produced on climbing stems, and but rarely on trailing shoots.

The stems of all the species are more or less woody below and herbaceous above. In temperate latitudes, the plant dies back to this woody base during the winter or dry season. If environmental conditions are harsh, the herbaceous stems may be greatly reduced and either semi-erect or prostrate; or, as in subg. Eusarcostemma, succulent, with the leaves reduced to scales. The plants usually are twining vines, extending from one to more than thirty meters into trees and shrubs.

The woody basal portion of the stem is covered with the ridged, yellow bark of loose texture which is more or less characteristic of the Asclepiadaceae. This bark is first produced at the nodes where there may be corky knobs or ridges decurrent upon the internodes. Above these first few centimeters, the stem is gray- or yellow-green and may be pubescent or glabrous. Even in the latter case, there is usually much pubescence in the axil of the leaves and on the buds. In some species, the young stems are extremely pubescent, becoming less so at maturity.

The number of lateral branches normally produced is variable, but is a good character for several groups of species. When the plant branches profusely, the lateral branches usually are intertwined with each other and the main stem. There seems to be little correlation between the amount of branching and the type of habitat, although plants growing in the open tend to be more branched.

The leaves in *Sarcostemma* are entire and opposite and, on the monopodial portion of the stem, they are strictly decussate. After an inflorescence has been produced, the stem becomes sympodial *(vide infra)* and the leaves of each sympodium member no longer are at right angles to those at the floriferous node next below. By far the majority of the species have cordate leaves with characteristic palmate or pedate venation. As a rule, leaf shape can be used to distinguish groups of species, but there is much variation in the length/width ratio. In the desert species of Eusarcostemma, the leaves are reduced to scales which sometimes are difficult to find, for they wither rapidly. In this connection, it is interesting to note that in S. *clausum,* and less frequently in S. *glaucum* (subg. Ceramanthus), of the dry, coastal habitats of western Peru and Colombia, the leaves often are much reduced in size. In these species, as well as in S. *cynanchoides* ssp. *Hartwegii* (of the same subgenus, but occurring in arid, southwestern United States), the leaves sometimes are caducous, the aspect of the plant then being superficially much like that of a slender S. *viminale* (Eusarcostemma).

Most commonly, the margins of the leaves are entire and somewhat revolute, but they are undulate in several species of two subgenera. This condition apparently is caused by the continued proliferation of the lateral meristems of the leaf after interstitial growth has ceased, and is quite variable in intensity. In S. *crispum*, strikingly undulate leaves are the rule in Texas, but the degree of crisping is much less to the south and west where there actually may be no sign of it. Greenhouse plants of S. *pannosum*, which has less pronounced crisping, may have distinctly undulate and quite plane leaves upon the same shoot.

In nearly every specimen, one finds at the base of the leaf on the ventral surface of the point of juncture of the main veins, a number of small, digitiform structures referred to as "glands" in the taxonomic literature (fig. 1). They are yellow or orange in color and vary in size with the vigor of the plant. In desert

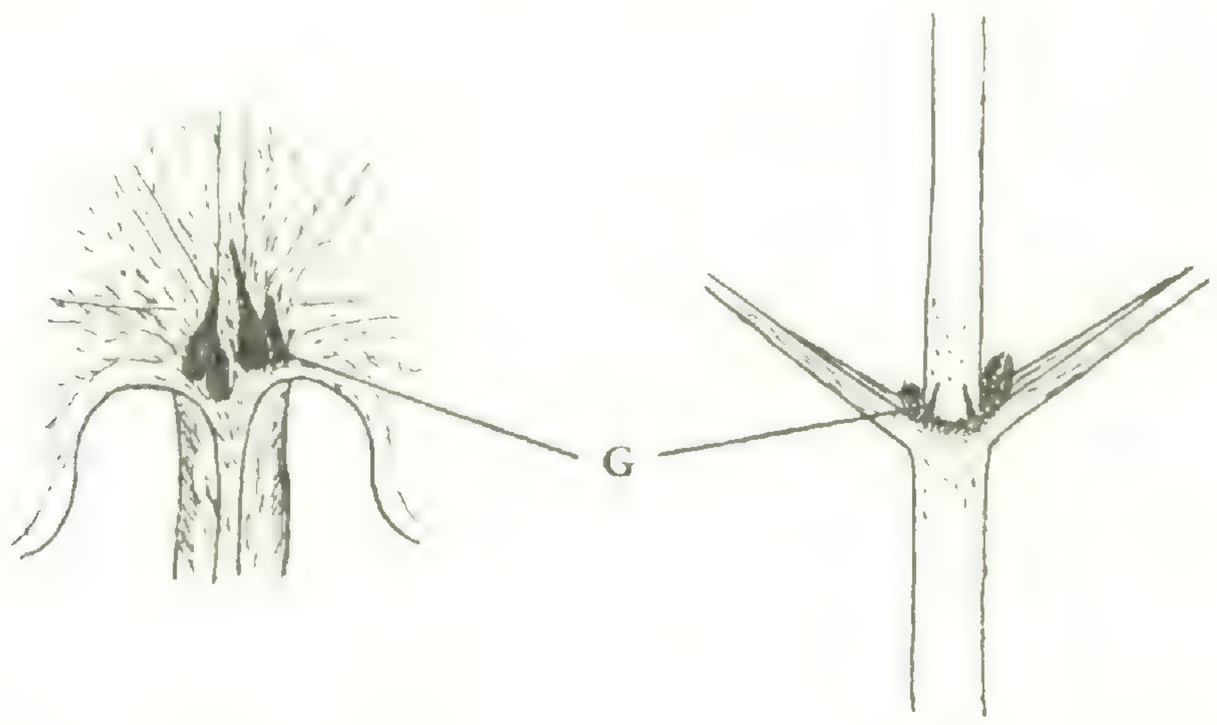

Fig. 1. Foliar glands: 1, base of blade; 2, node; G, gland.

species they usually are reduced in size or occasionally absent. Similar "glandular" structures are found at the nodes, lateral to the petioles, where their position and arrangement suggest that they are reduced stipules; this view is further supported by the fact that occasionally they are slightly laminate. The foliar "glands" are of no taxonomic significance, and their morphological or physiological importance is uncertain. As in the Apocynaceae, the petioles are connected by an interpetiolar ring which appears as a fleshy excrescence of the subjacent internode (fig. 1). The petiolar "glands" are inserted upon the edge of this ring, which also may be puberulent, especially adjacent to the petioles. When the stipular appendages are lacking, there often are tufts of hairs in a corresponding position.

There now can be little doubt that the inflorescence in the Asclepiadaceae is basically terminal, despite the considerable controversy which has taken place in the past. Anatomical, morphological, and experimental studies[29] are fairly clear

[29] cf. Demeter, in Flora 115:130–176. 1922; and Schoute, in Rec. trav. bot. Neerl. 34:182–204. 1937, each with a comprehensive bibliography.

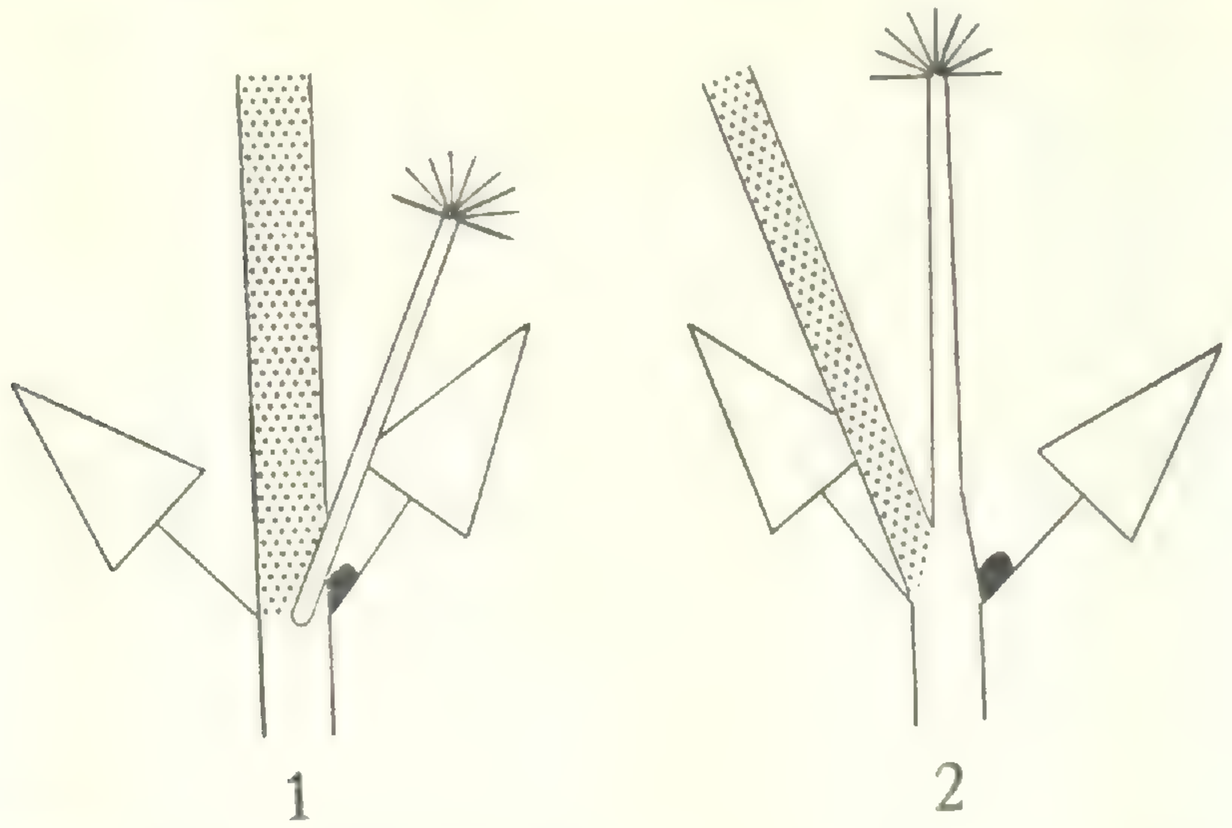

Fig. 2. Diagrams of inflorescence-bearing nodes: 1, actual appearance; 2, morphological interpretation; shading indicates axillary growth.

on this point. The axis which continues the growth of the plant after the first inflorescence arises from one of the buds of the last vegetative node, as is diagrammed in fig. 2. According to the unfortunately highly formalized interpretation of Schoute[30], subsequent sympodium members arise from the axils of the β-prophylls. This is only another way of stating that, with continued inflorescence production, each succeeding internode arises from one of the first two, opposite, leaves ("prophylls") of the node next below; there are, of course, no more than two leaves on this shoot.

Inspection of a vegetative shoot of *Sarcostemma* (fig. 3) shows that the buds in the axils of the paired leaves differ markedly in size; in fact one may be absent altogether. This is the rule in the Asclepiadaceae. If we consider the small buds and large buds separately, we find that they form two opposed spirals with 90° divergence. The first inflorescence terminates this monopodial axis, but is pushed aside by the vigorous growth of the large bud of the last leaf-pair. This shoot forms the first sympodium member, as the upper portion of fig. 3 indicates. The small bud in the axil of the other leaf sometimes grows, but rarely equals the main shoot. The reproductive phase, once initiated, continues indefinitely, each sympodium member bearing two leaves and an inflorescence. The rectangular crossing of the leaves is replaced then by a skew-crossing, for two of the angles between rows of leaves are obtuse and two are acute. As a result, the inflorescences, which are interpetiolar but nearest the large bud of the associated pair of leaves, are borne in two nearly straight rows on opposite sides of the stem, diverging from one another at 150–180°. The bud near the inflorescence is, of course, that which formerly was denoted as a "small" bud, for the large bud has become a sympodium member. A disturbing feature is the presence of an additional bud in the axil of the leaf which presumably subtends the main axis. This bud, which Schoute[31] dismisses as a "small accessory bud," I take to be of the nature of those which are present in such genera as *Juglans*, and which also have been reported for the

[30] Schoute, loc. cit. 1937.
[31] Schoute, loc. cit. p. 187. 1937.

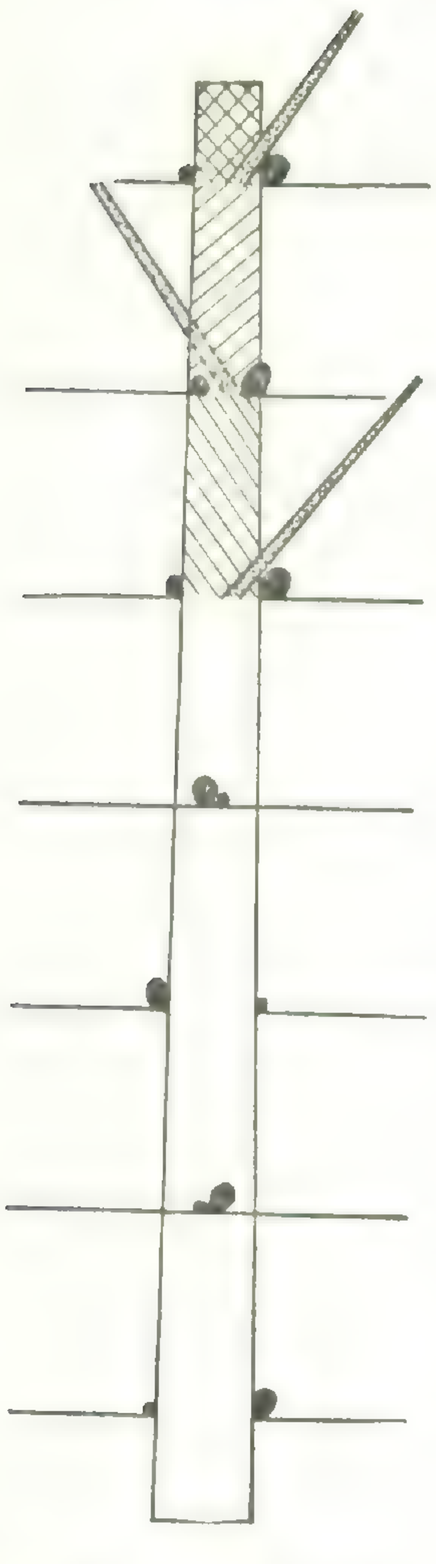

Fig. 3. Diagram of portion of stem of *Sarcostemma* showing large buds and small buds and arrangement of the inflorescences; shading indicates successive internodes of axillary growth.

Apocynaceae. In *Sarcostemma,* the presence or absence of the accessory bud varies both between and within species. Its absence appears to be correlated with a desert or open habitat.

Should the vegetative phase be resumed after a period of inflorescence production, the axis again becomes monopodial and the leaves strictly decussate. It is hardly necessary to add that the torsions introduced by the voluble habit greatly obscure the details of inflorescence and leaf arrangement which are sufficiently difficult to follow on the stem of erect forms.

This condition of the inflorescence is a general one throughout the Asclepiadaceae, and may be noted even in such modified forms as *Stapelia.* In those genera where the inflorescence appears to be axillary, it may be interpreted as terminal according to Schoute. Very rarely, as in *Sarcostemma angustissimum,* the inflorescence actually is terminal to the main axis or a lateral branch. Only one floriferous lateral branch is produced at a node in the latter case. It appears plausible to consider this a case of reduction and specialization, rather than one of primitiveness.

The type of inflorescence is quite variable in *Sarcostemma.* Usually it is umbelliform in subg. CERAMANTHUS and racemiform in EUSARCOSTEMMA and OXYSTELMA. The basically cymose nature of the inflorescence is demonstrated by the irregularly centripetal development of the flowers and by the arrangement of the flowers upon the floriferous axis.

In the subg. CERAMANTHUS, the type of inflorescence has been used to distinguish four series. *Sarcostemma pannosum* is placed in a series by itself since the inflorescence always is manifestly compound. The nodeless peduncle may dichotomize in extreme cases producing two cincinni, each more than a centimeter in length. Upon the axis the flowers are disposed spirally in pairs.

A second series includes S. *clausum* and S. *glaucum* in which the peduncle ordinarily equals or exceeds in thickness the axis below the inflorescence-bearing node. Frequently it bears two catenulate cymes; the inflorescence is umbelliform, all the flowers appearing to come from about the same place, but blooming in an irregularly centripetal fashion. The second cyme, if present, is lateral and sessile upon the peduncle.

Most of the species of subg. CERAMANTHUS fall into a third series in which the inflorescence is umbelliform and is borne upon a slender peduncle which only very rarely equals the stem in thickness or bears a secondary cyme. *Sarcostemma angustissimum* is placed in a monotypic series on the basis of its terminal inflorescence; the peduncle is short or absent, but when present is not equal to the stem in thickness.

The inflorescence in subg. OXYSTELMA most commonly is racemiform, although the superficial appearance of occasional individual plants may belie their structure. Thus while all of the species with racemiform structure may experience such abbreviation of the floriferous axis as to simulate the umbelliform type in one or more inflorescences, comparison of a number of inflorescences, or careful examination of the peduncle for bracts, will reveal the racemiform nature. On the other hand, *Sarcostemma solanoides* presumably never deviates from the strictly umbelliform inflorescence. *Sarcostemma* (§ PENTACYPHUS) *andinum* apparently illustrates reduction from the racemiform type along different lines: invariably there are two nodes in the inflorescence, each of which bears a single flower. Again it must be realized, however, that specimens of species with typically racemiform inflorescences (which have the flowers arranged in pairs along an axis of several nodes) may assume this appearance. The nature of the inflorescence has not been used to delimit series in OXYSTELMA since the species do not seem to fall into natural groups along these lines.

In all the species of *Sarcostemma*, there is a tendency for a more or less specialized reproductive portion of the axis to be developed. This condition is most clearly seen in S. *clausum* and S. *glaucum* where the inflorescences may be borne upon long, lateral branches which have reduced leaves, the whole resembling the compound inflorescences of certain species of *Cynanchum (Tassadia)*.

Length of the peduncle is a character which has been used with disastrous results in the past, as a glance at the synonymy of S. *clausum* will testify. Many of the segregates of that species were based upon slight differences in the length of the peduncle relative to the associated leaves. Within several species the peduncle may be much longer than the leaves or absent entirely. In certain species, however, the extreme conditions are valid characters, e. g. in S. *elegans* vs. S. *Torreyi*.

Few distinctive features are presented by the pedicels. Relative number, thickness, and length are of some value in setting apart groups of species, but have little practical use. The pedicels elongate gradually until anthesis, and if fertilization takes place and a fruit is formed, the pedicel and peduncle enlarge to support the follicle.

The calyx in *Sarcostemma* is gamosepalous, and the lobes are divided nearly to the base. The upper surface usually is glabrous, but the lower varies from glabrous to densely pubescent. In many cases, especially in subg. CERAMANTHUS, the marginal hairs are long, making the lobe ciliolate. Within the calyx tube, generally distributed about the base or alternating with the lobes, are one or more digitiform

structures commonly called "glands." These apparently are homologous with the calycine squamellae of the Apocynaceae which have been interpreted as being of stipular origin[32]. In the apocynaceous genera studied, they were correlated with the nature and arrangement of the stipules and were constant within a genus or subgenus. No such correlations have been noted in *Sarcostemma;* the number and distribution of the squamellae are variable and without taxonomic significance. A squamella consists of a central core containing many druses and an outer, deeply-staining, palisade epidermis.

It would appear that where reduction in size of certain structures has proceeded to a given point, they assume this more or less cylindrical, translucent, lutescent appearance of the "glands." This may be noted, for example, for the stipules. Occasional aberrancies also are suggestive: in one specimen of *S. clausum*, a single calyx lobe had a "glandular," lateral appendage at the base: in *S. angustissimum*, the minute calyx lobes are "glandular" at the apex; in *S. lysimachioides*, the squamellae are borne in groups at the margin of a triangular pad of tissue alternating with the calyx lobes; finally, in those species with mucronate leaves, the mucro often is strikingly similar to the various "glands" in appearance. On the other hand, there is some indication that the multicellular hairs found upon the interpetiolar ring and the calyx lobes may become "glandular" in appearance. The whole problem is one which would repay investigation, for upon its solution depends our interpretation of the calycine squamellae and the appendages of the leaves.

The corolla is gamopetalous, and the degree of cohesion of the lobes is an important taxonomic character. In general, species of subg. OXYSTELMA have very broadly campanulate corollas which are shallowly lobed; in the angles of the sinuses there often are minute petalaceous teeth. The corolla in subg. CERAMANTHUS and EUSARCOSTEMMA is rotate-subcampanulate or salverform and is divided nearly to the gynostegium. The corolla lobes usually are spreading or ascending, but they may be strongly reflexed.

It is the behavior of the androecium and gynoecium which characterizes the Asclepiadaceae as a family, hence it will not be amiss to describe in some detail the morphology and anatomy of the structures in these two floral whorls. The material on which the following discussion is based consists of longitudinal and cross sections of flowers and buds; extensive use also has been made of flowers and buds cleared in 5 per cent sodium hydroxide solution and treated with lactic acid. The latter technique is especially useful, for the sodium hydroxide removes all coloring material from the tissues rendering them transparent; the cell walls, however, are undistorted and may be studied with or without the application of a stain.[33] In such preparations, the course of the vascular bundles may be followed *in situ* and a clearer concept of the spatial relations of the various parts may be obtained without the laborious method of reconstructing from a series of sections.

[32] Woodson, R. E., and Moore, J. A., in Bull. Torr. Bot. Club 65:135–166. 1938.

[33] This technique is described in A. S. Foster's 'Practical Plant Anatomy,' 1949. Staining is discussed by Thomas Morley in Stain Techn. 24:231–235. 1949.

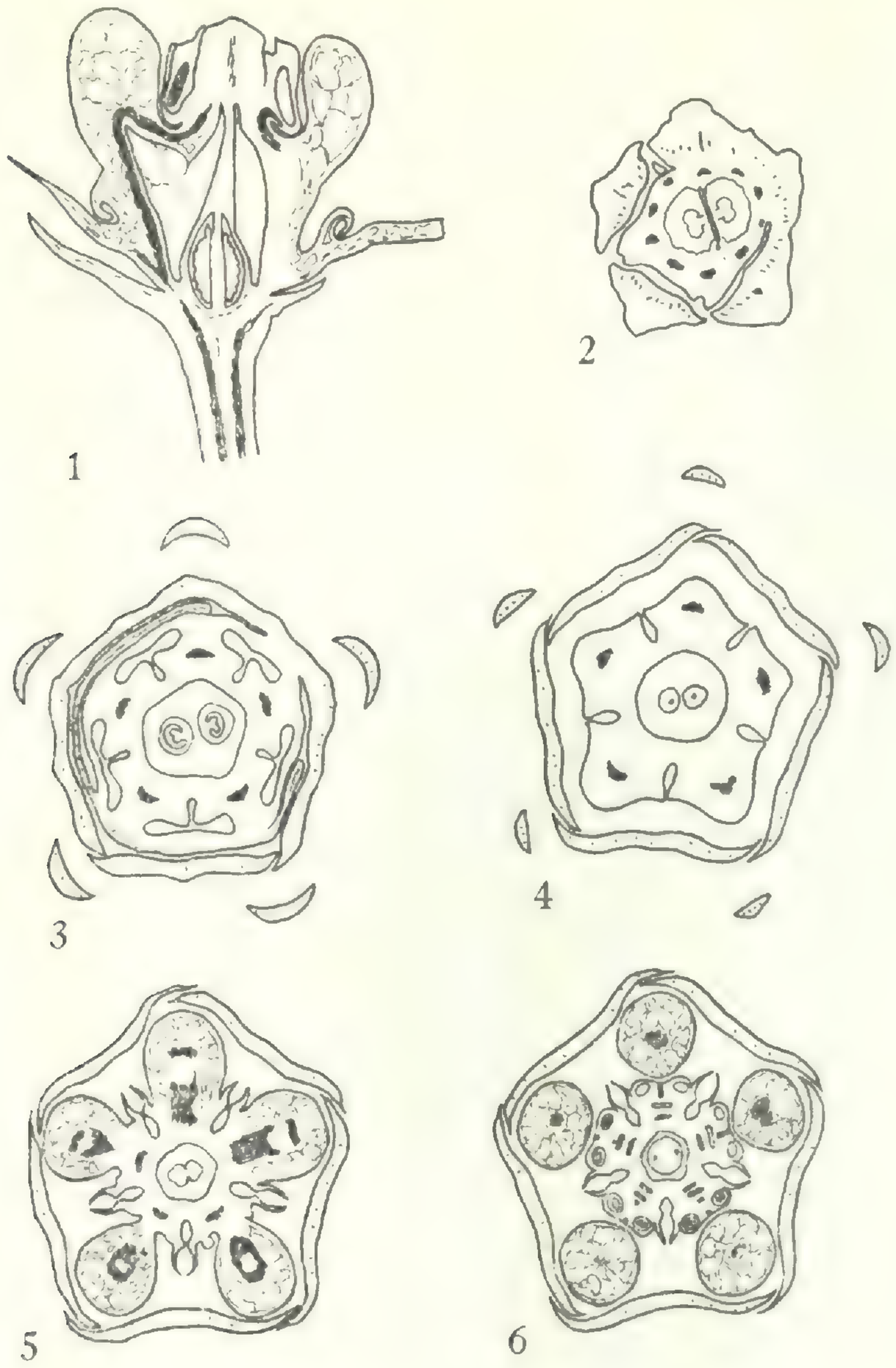

Fig. 4. Longitudinal section of flower and cross section of bud: 1, longitudinal section of flower showing vascular bundle of stamen, ring of the corona, and slightly immersed carpels; 2, cross section through receptacle showing sepals, squamellae, and carpels immersed in the receptacle; 3, cross section through the region of the corona ring showing ring, corolla, and the staminal column; 4, cross section through the staminal column showing grooves and the styles; 5, cross section through the region of the corona vesicles showing vascular bundle in the corona vesicles and the anther-wings; 6, cross section through the gynostegium above the attachment of the corona vesicles showing the thecae and pollinium-sacs, anther-wings, and the base of the stigma-head.

Supplementing the description which follows are the semi-diagrammatic drawings of fig. 4 which represent cross sections of a bud, and a longitudinal section of a flower of *Sarcostemma pannosum*. The five antesepalous stamens are borne upon the corolla tube near the base and are coherent laterally almost to their apices, forming an epipetalous tube. The united filaments constitute what commonly is called the column. Externally, the filaments are marked by deep grooves in the

column in subg. CERAMANTHUS and EUSARCOSTEMMA, but these usually are lacking in OXYSTELMA. In *S. andinum*, the margins of the groove are extended at an angle of about 45° to the column, forming two prominent flaps continuous with the anther-wings.

The anthers contain but two pollen-sacs, each of which is visible dorsally as an elongate protuberance. The connective is prolonged into a short spike which supports a membranous margin. This apical appendage of the anther usually is appressed to the stigma-head. Ventrally, the anthers are coherent by their margins except for a short distance at the apex. The five sinuses thus produced in the staminal tube expose the receptive surface of the stigma, as will be discussed below. Laterally also, but abaxial, the margins of the anthers are produced to form the anther-wings or anther-alae. These are continuous with the margins of the groove in the column from which they differ markedly, however. Histologically, the transition is marked by a change in the composition of the cell walls as is indicated by their greater affinity for basic dyes (e. g. safranin).

Morphologically, the anther-wings are characterized by their cartilaginous texture and appearance, and by the fact that they are produced somewhat beyond the margins of the groove in the column. They are inclined at an angle of about 45° to the plane of the thecae and are recurved so that their edges are closely appressed. Towards the base there is an opening into the so-called alar chamber delimited ventrally by the conjoined anthers and laterally by the anther-wings. This orifice varies in size and shape from thin and narrow to large and circular. It is the opening into which the instrument of pollination is introduced.

As in all Cynanchoideae, the stamens at maturity are closely connivent with the united stylar region of the carpels (referred to as the stigma-head). While it is stated commonly that the anthers are merely loosely connivent with the stigma-head or united only by their tips, neither of these descriptions is accurate. The young anthers are at first free from the gynoecium. Fairly early in their development, however, the ventral surface of the staminal tube bulges to form a pronounced flange about the circumference of the staminal tube at the level of the locules. This flange in later development becomes closely appressed to the lower surface of the stigma-head and the tissue of the two structures finally becomes joined. It can be seen in sections of the flower that the cells of one dovetail between those of the other and that there is a slight crushing and disruption of the superficial layers. In this area, the highly differentiated, columnar epidermis of the stigma-head is unchanged in the bud stage, but by the time of anthesis, the cells have lost their characteristic rectanguloid shape and their strong affinity for stains. The anthers are free from the stigma-head around its entire circumference except at the flange. The lateral surface of the stigma is exposed, however, only at the five sinuses in the staminal tube, which are hidden within the alar chambers.

We come now to those structures of the androecium which collectively make up the corona. Woodson[34] has pointed out the dangers of lack of precision in the use of the word corona, which he rightly applies to "various elaborations or enations of the staminal filaments only." That definition is followed in this paper for the reason that there are at least three structures which have been, or could be, interpreted as corona in *Sarcostemma.* It is customary to speak of inner and outer corona, but there is no assurance that the "inner corona" of one group is not the equivalent of the "outer corona" of another, nor that it will not be mistaken for such by the user of the, at first sight, obvious key character. In many genera of the Asclepiadaceae, there are three appendages of the stamens, as well as others of the corolla, so that any distinction of "inner" or "outer" corona becomes impossible.

In nearly all the species of *Sarcostemma,* there is a so-called "outer corona" or "faucal annulus." Whether this structure pertains to the corolla or to the androecium is not easy to determine; indeed, I am not certain what evidence could be considered definitive in the light of recent studies of the development and initiation of floral parts. The ring of the corona is best studied in the species of the subgenera CERAMANTHUS and EUSARCOSTEMMA, where it reaches maximum development. In subg. OXYSTELMA, the ring is present but usually abbreviated or adnate to the corolla. The corona ring may be a ridge at the base of the staminal column or a thick, revolute fold of tissue free from the corolla except at the very base. In many species, the ring is adnate to the androecium directly below the anthers; in others it is adnate to the corolla; finally, there are species in which the ring is adnate both to androecium and corolla. Cross and longitudinal sections show that the ring is more or less double at maturity and is composed of the same type of rather loose parenchyma as are the corolla and corona vesicles borne upon the filaments. No vascular supply is present, nor does the staminal trace diverge from its course in the direction of the ring. Viewed superficially, the corona ring is similar in texture to the androecium and not to the corolla. In subg. OXYSTELMA, § EUOXYSTELMA, both the column and corona ring are often puberulent, while the corolla is glabrous.

In the hope that developmental studies might shed some light on the problem, sections of buds and buds of varying age, cleared with sodium hydroxide, were examined. The later development of the flower studied here is remarkably similar to that described by Boke[35] for *Lochnera rosea.* As in that species, it is possible to distinguish two portions of the corolla tube: that below the insertion of the stamens, and that above this point. The lower corolla tube in *Sarcostemma* appears to be of receptacular origin, as is the case in *Lochnera.* The corolline traces do not branch until they reach the point of staminal insertion, whereupon two laterals depart simultaneously from each, run periclinally to the margins of the lobe, finally

[34] Woodson, in Ann. Mo. Bot. Gard. 28:199. 1941.

[35] Boke, Norman H. A series of three papers in Am. Jour. Bot. 34:433–439; 35:413–423; 36:535–547. 1947–1949.

to pursue their customary course upwards. A number of secondary branches from the distal margin of the horizontal portion of the laterals supply most of the mesophyll of the corolla lobe. Distal to the androecium, the upper corolla tube appears to be the result of ontogenetic fusion of separate lobes. The two lateral veins are closely appressed and traces of former epidermal layers often can be made out, especially near the sinus. The proximal portion of the upper corolla tube is slightly thickened by an adaxial meristem of the sort noted by Boke.

Unfortunately, the origin of the corona ring is not clarified by a study of development because of its early association with both the upper corolla tube and the staminal column. As nearly as I can determine, it arises in the angle of the sinus formed by the insertion of the stamens upon the corolla. Opposite a stamen, the ring appears first as a protuberance from the column; opposite a corolla lobe it appears in the sinus (in the bud stage).

Though the evidence is by no means clear-cut from this preliminary work, I am of the opinion that the corona ring must be considered a part of the androecium if we are to attempt to assign such structures to one of the formal categories of descriptive morphology. Comparison of *Sarcostemma* with a number of other forms in the Cynanchoideae shows that many have a tendency, expressed to a greater or lesser extent, for the base of the staminal tube to flare out into a corona ring, e. g. *Fischeria, Gonolobus,* and other genera, especially of the Gonolobeae. Perhaps the corolline faucal annuli of such forms as *Stapelia* and *Periploca* are the result of growth of the adaxial or ventral meristem discussed by Boke and Troll.

The so-called "inner corona" is composed of five vesicular outgrowths of the filaments directly below the anthers. Since the corona, as I interpret it, comprises both the ring at the base of the column and these enations of the filaments contiguous to the anthers, I shall refer to its components as corona ring and corona vesicles. The vesicles are constituted of a loose parenchyma which becomes distorted during later growth. They arise late in ontogeny so that in a bud, even shortly before anthesis, they may be quite small. Incidently, this has led to the description, in other genera, of species "*parvicoronata*," etc. based on nearly mature buds. Towards the base of the vesicle, the staminal trace usually arcs strongly upwards into the corona segment before reaching the anther.

The corona vesicles arise as small protuberances increasing in size gradually by interstitial growth, for the most part. Shortly before anthesis, rapid growth ensues, principally in the epidermal and immediately subjacent layers. The deeper-lying cells are stretched to form an aerenchyma and may be grotesquely twisted. Probably it is the inclusion of innumerable intercellular spaces filled with air which gives to the vesicles their characteristic, almost crystalline, appearance.

The corona vesicles are quite variable in shape. At the opening of the flower they are ovoid or obovoid, occasionally somewhat quadranguloid or laterally compressed. The upper end is rounded, truncate, or pointed; frequently there is an apiculation on the inner side at the apex. In subg. OXYSTELMA § EUOXYSTELMA,

the corona vesicles are attenuate apically, forming long, incurved processes exceeding the stigma-head. Towards the base, there may be manifest a decided constriction above the attachment of the vesicle to the column. The latter forms a sort of platform supporting the vesicle in many species.

Variation in the corona vesicles has been much over-emphasized taxonomically in the past, although the dangers of such a course have been stressed by most authorities on the family. Examination of herbarium material of all the species, supplemented by greenhouse and field observation of a number, has convinced me that, while the corona-shape potentialities are constant in the species recognized here, developmental upsets of one kind or another may modify their actual shape considerably, especially in subg. Oxystelma (cf. S. *Gilliesii* and S. *campanulatum*). The presence or absence of an apiculation, or the degree of compression, must not be overly stressed where individuals are concerned.

All these elaborations of the androecium apparently have arisen as a result of natural selection operating in conjunction with entomophily. The method of pollination recently has been described and illustrated for *Asclepias*[36] and a detailed discussion is not necessary here. The essentials of the process are well known, but a clear understanding must await sedulous biological study. It is speciously simple to assign roles to the various components of the complicated flower, but many aspects will have to be re-examined. For example, it is seldom realized that in most cases the corona and other floral appendages serve not so much to attract insects as to guide their legs into the proper position for pollination. In its search for the abundantly secreted nectar (which is well advertised by a heavy fragrance), an insect scarcely can avoid getting its feet or various bristles upon its body caught in the anther-wings at the basal opening. Once caught, there is no escape without withdrawing a pollinium.

According to the terminology which I shall employ, each pollinium consists of two pollinium-sacs which are joined by the translator arms (or caudicles) to the corpusculum. The translator arms and the corpusculum, sometimes called the "gland," make up the translator apparatus. Each pollinium-sac consists of the contents of one locule of the anther, enclosed by a yellowish, elastic substance of a waxy appearance. This investing layer about the pollen apparently is secreted by the tapetum at an early stage in development. The pollinium-sac is essentially oblongoid-cylindrical, but gibbous in outline, and the more strongly curved edge is toward the connective of the anther. At the time that the pollinium-sacs are being formed, the glandular surface of the stigma-head is secreting a substance not unlike that surrounding the pollen. While this process has been described both in English[37] and in German[38], the details are not known widely. The essentials have been confirmed for *Sarcostemma*. The result of this secretion, deposited at

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[36] Woodson, op. cit. 198–199. 1941.

[37] Corry, Thomas H. Structure and development of the gynostegium and the mode of fertilization in *Asclepias cornuti* Decne. (*A. syriaca* L.), Trans. Linn. Soc. II, 2:173–207. 1884.

[38] Demeter, Karl. Vergleichende Asclepiadeenstudien. Flora, n. s. 15:130–176. 1922.

varying rates and times, is the translator apparatus, one of the most remarkable structures in the plant kingdom.

That portion of the stigma-head above the alar chamber is creased by a furrow along the same axis as the anther-wings. The margins of this furrow secrete first and they form two bars of a substance which, initially soft and yellow, hardens and becomes deep brown. Subsequently the entire furrow begins to secrete, and the two bars thus become connected at the back by a thin plate. At the same time, however, the stigma-head is developing and slowly changing in size and shape: by differential growth, the margins of the furrow and their secreted bars are pushed forward and toward one another as the furrow increases in size at the back. The corpusculum at this stage is in the form of a clip, the free ends curving inwards. It is easy to see, then, why the name "gland" is inappropriate for the corpusculum, for it not only secretes nothing itself but is scarcely adhesive as was formerly believed.

Rather late in development, two bands of tissue of the stigma-head, extending from the corpusculum to the pollen-sacs of contiguous anthers, secrete the material which forms the translator arms. Because of their relative thinness, the translator arms clearly show the imprint of the epidermal cells which secreted them; the result is that they appear cellular to superficial observation. The corpusculum, on the other hand, is so thick that it is only in sections or whole mounts cleared in lactic acid that one can discern the slender bars of secrete of which it is constituted. In carefully made sections these may even be referred to the cells from which they were produced.

Several days before the bud opens, the ventral wall of the anther begins to disintegrate across a relatively wide area at the apex of each locule and this continues until each pollinium-sac is exposed at the back. The distal end of the caudicle, being the last portion to be secreted and protected from desiccation, is still soft and adhesive, and it apparently contacts the upper corner of the pollinium-sac and fuses with it. In *Sarcostemma,* there is a perceptible joint between the two separately formed structures. In other genera, however, the translator arm merges gradually with the substance of the pollinium-sac envelope. At the time of anthesis the translator arms are soft and flexible, and because of a difference in thickness of the secreted material and of the curvature of the stigma-head have developed a torsion which causes them to turn at right angles to the plane of the corpusculum, when removed from the flower. By this motion the attached pollinium-sacs are caused to rotate 90° so that the more convex side is turned toward the back. Thus it comes about that the two bags of pollen lie in parallel planes instead of in the same plane as they did in the flower.

The corpusculum usually is broadly sagittate, but may be narrowly so, or ellipsoid. As a consequence of the method of its secretion, it is canaliculate and the canal, in the form of a cone, is open along the front forming a cleft. The latter is aligned with the alar chamber so that if a bristle of the proper size is introduced into the alar chamber at the base and pulled upward, it is drawn into

the corpusculum and wedged firmly in the cleft. When withdrawn from the flower, the bristle then carries with it the pollinium, the two pollinium-sacs rotating slowly as the caudicles dry. Should the same bristle be inserted similarly into another alar chamber, it is the translator arm attached to one pollinium-sac which is caught in the anther-wings, while the other remains outside of the chamber. At the top of the alar chamber the pollinium-sac is abruptly caught against the projecting stigma-head and it breaks from the translator arm. The latter, thus freed, passes into the cleft of the corpusculum of the new pollinium, which is then withdrawn. This process of insertion and removal produces the dichotomous or unilateral combinations of pollinia called multiple pollinia. I have observed multiple pollinia composed of more than twenty pollinia; and, in one instance, a small insect formed a bridge between two pollinia.

Judging from the relatively high frequency with which they occur in the species which I have examined, multiple pollinia are a regular and natural occurrence in many asclepiads. Robertson[39] has discussed the importance of multiple pollinia to species of *Asclepias* with large gynostegia which catch fewer processes on an insect's leg. In such cases, they afford a greater chance of insertion since broken caudicles appear to be more easily caught than insect bristles and since the long multiple structures are guided more efficiently into the anther-wings by the corona segments. By means of multiple pollinia an insect can carry many more pollinia than the available bristle space would allow were each bristle to bear but one corpusculum.

When described, the process of pollination seems hopelessly complex and laborious, yet when the proper instrument of pollination is employed it is surprisingly easy to perform. In *Sarcostemma bilobum* ssp. *Lindenianum*, for example, where the orifice of the alar chamber is sufficiently large to admit a fine dissecting needle, I have produced multiple pollinia with little difficulty; a fine hair is suitable for species with smaller flowers. Brown[40] and Robertson[41] have noted the amazing rapidity with which the proper insect is able to effect pollination. Often the action is quicker than the eye can follow. If one watches the flowers for even a short period he is certain to see many insects, attracted by the sweet fragrance, crawling over the umbels of flowers and probing for nectar among the corona segments. The weight of the insect makes the flower, or entire inflorescence, suddenly top-heavy, and, as it begins to tilt, the insect grasps the only structures which afford support, the projecting anther-wings. Rarely is an entire leg caught by the alar chamber; usually only a bristle or row of setae upon the leg or abdomen slips into the orifice, and with a single swift movement of the insect, a pollinium is withdrawn. Pollination is only slightly more difficult, requiring the insect to give an extra tug which breaks the pollinium-sac from the caudicle.

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[39] Robertson, Charles. Insect relations of certain Asclepiads. I. Bot. Gaz. 12:214. 1887.
[40] N. E. Brown, in an appendix to Corry, op. cit. 1884.
[41] Robertson, Charles. Notes on the mode of pollination of *Asclepias*. Bot. Gaz. 11:269. 1886.

I should mention that in *Sarcostemma* the majority of mature flowers taken from herbarium specimens were found to have been pollinated at least once. Usually no more than three pollinia are inserted into the alar chambers of a single flower, but it is by no means uncommon to find a flower completely pollinated. Only very rarely have I seen a single pollinium-sac removed from its locule with the other still in place, and I have never observed a pollinium-sac which had produced pollen tubes while still within the locule.

It would appear that cross-fertilization is the rule in those species of Asclepiadaceae which have been studied. Some, like *Asclepias syriaca,*[42] *A. curassavica,* and *A. nivea*[43] are self-sterile. In others it appears likely that the behavior of the translator arms in turning the pollinium-sacs into the right plane for insertion between the anther-wings, a matter of one or two minutes time, would lead to cross-pollination, even if there were no other mechanism for insuring this.

The family Asclepiadaceae has been divided into two sharply distinct subfamilies on the basis of the structure of the translator apparatus and related floral differences. The pollinia of the Cynanchoideae, described in preceding paragraphs, may be visualized to have evolved from simpler structures in the Periplocoideae and Apocynaceae according to the interesting studies of Demeter.[44] In the genus *Apocynum* (Apocynaceae), the first semblance of a translator apparatus is found. Here the stigma-head secretes five thin, quadrangular plates which alternate with the stamens. These are enclosed within cartilaginous margins of the anthers (similar to the anther-wings) and are adhesive, catching the pollen which is discharged from the anthers in tetrads. This pollen-bearing structure then becomes stuck to the appendages of insects which visit the flowers and thus disperse the pollen.

The Periplocoideae also discharge the pollen in tetrads. The latter fall from the anthers into rather complicated translators which are divided into three parts: an upper spoon- or cone-shaped structure which is adhesive and contains the tetrads, a lower adhesive disc which becomes attached to the insect, and a central connecting stalk. After studying the method of formation of the translator and certain teratological forms, Demeter[45] concludes that the spoon or cone is homologous to the corpusculum and that the adhesive disc is comparable to laterally conjoined translator arms. Changes in the shape of the stigma-head and in the distribution of the secretory cells can be imagined which would lead to the formation of a typical pollinium.

Although the occurrence of pollen grains grouped into tetrads is scattered throughout the flowering plants, the formation of pollinia has been reported only for the Asclepiadaceae, the subfamily Mimosoideae of the Leguminosae, and the

[42] *cf.* Stevens, O. A. Cultivation of milkweed. N. Dak. Exp. Sta. Bull. 333. 19 pp. 1945; and Sparrow, K. K. Types of pods of *Asclepias syriaca* found in Michigan. Jour. Agr. Res. 73:65–80. 1946.

[43] I have been unable to self-pollinate or to hybridize *A. nivea* or *A. curassavica* in the greenhouse, despite repeated attempts.

[44] Demeter, op. cit. 174. 1922.

[45] Demeter, loc. cit.

Orchidaceae. In the Chlaenaceae, a small family of the Malvales, there are multiple groups of four or sixteen pollen grains enclosed within a deeply furrowed wall.[46] This wall has been interpreted as the modified spore-mother cell wall, and, if this interpretation is correct, these aggregates cannot be referred to as pollinia (as their describer recognizes). The pollinia of the other three groups are characterized by having the pollen grains merely adherent, with or without a thick matrix, and not enclosed within a single cell wall.

In the Mimosoideae, the pollen is in tetrads or aggregated into pollinia of relatively few grains, in an ovoid mass which bears at the pointed end an adhesive substance apparently derived from the tapetum. The stigma is a simple, obscurely sulcate, capitate structure, and there are no special devices for receiving the pollinia.

The Orchidaceae show an interesting series from pollen in tetrads to various types of pollinia. In the more primitive forms each locule produces many small pollinia similar to those of the Mimosoideae, but these are held together into packets by viscid threads derived from the tapetum. These compound pollinia may be attached by slender, elastic caudicles to an adhesive disc which is the secretion of the rostellum, a sterile portion of the stigma. In certain species, the sticky substance secreted by the stigma is first applied to the head of a visiting insect, and the pollinia subsequently fall from the anthers into this substance and become affixed. Pollinia of the more advanced type are compact, waxy structures borne upon rather specialized caudicles which are attached to an adhesive, cellular disc. In this case, a layer of tissue of the rostellum has abscissed, carrying with it the sticky secretion. The caudicles undergo various movements which put the pollinium into the proper position for pollination.

In general, the pollinia of the orchids are much less specialized than those of the Asclepiadaceae. The rostellum is, in a sense, comparable to the secretory stigma-head, and the caudicles and adhesive disc have been compared with the translator arms and corpusculum of the asclepiads. These similarities are rather superficial, however. Furthermore, the structure of the stigmatic chamber in the orchids is by no means as directly related to that of the pollinia as it is in the milkweeds, a fact which perhaps accounts for the more frequent occurrence of natural hybrids in the orchids in contrast to the asclepiads. On the other hand, in the transformation of the perianth into the most outlandish structures, and in the development of special insect food tissues or of pseudocopulation, the orchids have far surpassed the Asclepiadaceae.

The Asclepiadaceae are often mentioned as illustrating mechanical isolation of species and extreme adaptation for insect pollination, but few persons have realized the delicacy and precision of the relationship. While pollination can easily be accomplished by the right pollinator, it must be emphasized that there are so many elements involved in the process that, if any one is incompatible with any other,

[46] Smith, C. C. A case of "pollinia." Phytologia. 1:83–88. 1934.

it fails. That most assiduous, but apparently almost forgotten work of Charles Robertson[47] has made this quite clear. Precisely to what part of an insect's body a pollinium will be attached is determined by the structure and height of the corona, the length of the column, the structure of the anther-wings, the structure of the stigma-head, the shape of the corpusculum, etc. Robertson[48], for example, found that bumble-bees may have pollinia of *Asclepias Sullivantii* on their claws, of *A. verticillata* on their tarsal hairs, and of *A. longifolia* on the hairs of the ventral surface. These three species, although in bloom at the same time and employing the same efficient pollinator, are nevertheless practically incapable of hybridization. While visiting a flower of *A. Sullivantii,* the bumble-bee deposits only pollinia of that species, because only they are in a position to be inserted and caught in the alar chamber. If it should happen that pollinia of *A. verticillata,* upon the tarsal hairs, were caught between the gaping anther-wings of *A. Sullivantii,* they are so small that they would be withdrawn without affecting the plant in any way. Conversely, the pollinia of *A. Sullivantii,* the flowers of which are about three times the size of those of *A. verticillata,* cannot be inserted into the alar chamber of the latter under the dissecting microscope, much less by the bumbling bee. Similar relationships are found between *A. longifolia* and the other two species; in size, the flowers approach those of *A. verticillata,* but the anther-wings and pollinia have a completely different structure.

Further evidence for the rigidity of the interrelation of flower and insect is provided by the multiple pollinia. I have never found these combinations to include more than one kind of pollinium (and the morphology of a pollinium often is sufficient to define a species in *Sarcostemma*). There is, thus, what might be called a lock-and-key relation between the pollinia and the alar chamber. It is only the proper key, the pollinium-sac, which can be inserted into a given lock, the alar chamber, so that fertilization will take place. Moreover, the key must be in the proper hands to gain access to the lock.

We may inquire into the effects of the intimate relationships between the milkweeds and their insect-pollinators, and although we cannot yet answer the question, we can perceive that the effects are far-reaching ecologically, genetically, morphologically, and taxonomically. The plant is dependent upon a particular type of pollinator, and both the plant and the insects in its environment must have evolved more or less together. *Sarcostemma pannosum,* from western Mexico, when grown in St. Louis was visited by many insects, but no pollinia were withdrawn and no fruit produced. A plant, on the other hand, may have a profound effect upon the insects, aside from that of supplying them with food. It is well known that insects sometimes are caught by the corpuscula which they are not sufficiently strong to remove, and they perish on the flower. Indigenous forms

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[47] Robertson, Charles. Notes on the mode of pollination of *Asclepias.* Bot. Gaz. 11:262–269. 1886. Insect relations of certain asclepiads. I & II. ibid. 12:207–216, 244–250. 1887; Flowers and insects, Asclepiadaceae to Scrophulariaceae. Acad. Sci. St. Louis. Trans. 5:569–577. 1891.

[48] Robertson, op. cit. p. 250. 1887.

must be caught rather rarely when one considers that the number of visitors to a single flower runs into very high figures. However, for the hive-bee, introduced into our fauna, the situation is different. In a period of seventeen days, Robertson[49] found 671 dead bees in the flowers of a patch of *Asclepias Sullivantii*. Furthermore, this species, which fastens its pollinia to the claws of insects, may so fetter a bee with pollinia that it is expelled from the hive as a result of its inability to collect honey and to climb upon the combs. Of course, *A. Sullivantii* is not benefited, for, as Robertson puts it: ". . . it seems that the flowers are better adapted to kill hive-bees than to produce fruit through their aid."

Genetically, a situation results in which the species are isolated mechanically from hybridization with one another, yet usually are cross-pollinated with other individuals of their own species. Two species, then, as isolated as if one had migrated into a different habitat, may respond with striking specializations in floral structure but undergo little or no change in vegetative organs. One need only compare species of *Gonolobus*, *Marsdenia*, and *Cynanchum* from Mexico or South America to see that often only slight differences, in the structure and arrangement of the trichomes, for example, distinguish them vegetatively. Yet the floral differences are so great that they are used to characterize categories of tribal rank.

This field of inquiry is one which still scarcely has been touched. It will require much patient field work before a picture of the dynamics of any one species can be worked out. A taxonomic monograph can serve to indicate some of the problems, however, and should function as a framework, albeit flexible, within which they are interpreted. It is of considerable interest to note that in several closely related species of *Sarcostemma* which occupy the same or contiguous areas, there are differences in the shape of the pollinium-sac and corpusculum and complementary differences in the anther-wings which would make hybridization very difficult. If one examines the key to the species of the series CYNANCHOIDES, he will notice how many groups of species are segregated by differences in the structure of the pollinium, the length of the column, or the degree of apiculation of the stigma-head. This, in all probability, explains the rarity of hybridization and those evolutionary processes associated with introgression which are proving to be of such importance in other families of plants and animals. Certainly the Asclepiadaceae offer fascinating subjects for the evolutionary biologist.

The conjoined stamens and gynoecium make up a structure called the gynostegium, the name referring to the fact that the androecium completely roofs over the carpels. The stigma-head exposed at the top is more complicated than might appear at first sight. The apex is papillate and may be obscurely bilobed or bear two long apiculae. The degree of apiculation, however, is somewhat variable, and characters of the stigma-head must be used with discretion. The rather massive body of the stigma-head contains two central strands of short, spirally thickened cells. These are a continuation of the vascular strands of the styles which gradually

[49] Robertson, op. cit. p. 211. 1887.

attenuate toward the apex only to enlarge within the stigma-head to form a core of considerable dimensions. Their function appears to be to support and to strengthen, since in other genera they extend nearly to the surface and, flaring broadly, form a subepidermal layer of sclereids.

The papillate apical portion of the stigma-head is distinct from a lower, non-papillate region which projects, shelf-like, laterally. On the upper surface of this area are the five furrows in which the corpuscula are secreted. Lateral to these are the less prominent grooves in which the translator arms are produced. Below this region the stigma-head is abruptly constricted to the styles. Upon this lower surface is the receptive surface of the stigma and below this, the attachment of the flange of the staminal tube.

Corry[50] has stated that the receptive area of the stigma-head is a continuous ring, similar to that in the Apocynaceae, above the attachment of the staminal tube. Whether or not this is so can be determined only by laborious experimentation; the fact remains that the stigma-head is functionally receptive only at the five points which are accessible to the alar chamber, i. e. alternating with the stamens. In order for pollination to be effected, a pollinium-sac must be drawn between the anther-wings at the base and up against the stigma-head where it breaks from the caudicle. In many species there are projecting ridges within the alar chamber which firmly grip the pollinium-sac and hold it in the proper position. In this moist chamber, the pollen tubes grow, in the form of a skein, into the stigma and down the styles to the ovary. Although apparently all of the pollen grains germinate, the pollen tubes are found to escape only from a rather small area along the more convex edge of the pollinium-sac, which is always the edge towards the stigma in the alar chamber. This occurs whether they are germinated in the flower or in a sugar solution.

The two carpels are free nearly to the base and are somewhat sunken in the receptacle. Alternating with them are two small papillae, the nature of which is completely unknown. Devoid of vascular tissue, they may be the result merely of compression of the receptacular tissue by the confining corolla tube, or the vestiges of carpellodes. Very rarely one finds that three carpels have been produced, but conditions within the lower corolla tube are so crowded that it is difficult to determine if the small papillae still are present. The anatropous ovules are borne upon axile placentas and the micropyles are directed outwards.

Ordinarily only one carpel of a pair develops into fruit, although two is the rule in several species. The paucity of fruit, as compared with flowers, has been attributed to difficulty in pollination. This clearly is not the case in the forms which I have studied, for not only is pollination a simple matter for the right insect, but it is not uncommon to find inflorescences in which a majority of flowers have young fruit. Yet, in these same species, only a single follicle, or several, is to be found in a mature condition in an inflorescence. The matter appears to

[50] Corry, op. cit. p. 175. 1884.

relate to nutrition rather than fertilization. Moore[51] attributes the collapse of pods in *Asclepias syriaca*, in part at least, to competition for food between the endosperm and the adjacent maternal tissue in the ovules.

The follicles in *Sarcostemma* are narrowly fusiform to obclavate, except for S. *pannosum* and the Argentine race of S. *clausum*, where they are inflated at the base. According to Teodoro Meyer[52], the corky, inflated follicles of this race of S. *clausum* are adapted for floating.

The seeds are unequally biconvex or complanate. Usually the dorsal side is more or less rugose, and the flatter, ventral side bearing the obscure raphe, minutely papillate. The margin is flattened and may be serrate at the chalazal end. The white or yellowish coma is produced at the micropylar end of the seed. In the Asclepiadaceae, the coma arises from the rim of the micropyle on the side toward the funicle and does not encircle the micropyle.[53] The presumptive papillae scarcely are apparent in the flower at anthesis, but after fertilization they undergo remarkably rapid growth to produce the apparatus for wind transport so characteristic of the family.

There are few reliable taxonomic characters in the fruit and seeds. It is only with considerable experience with a genus that one can safely identify fruiting specimens in the Asclepiadaceae.

Geography

While particular geographic problems will be discussed under the species to which they pertain, it may be of interest to present a general picture of the distribution of *Sarcostemma*.

The subgenus Ceramanthus includes species from southwestern United States to northern Argentina. The center of diversity is in Mexico, from whence the species extend into more or less xeric habitats, at low to moderate altitudes, to the north and south. In northern Mexico and in the southwestern United States, the plants inhabit dry, sandy washes or arroyos, and they show morphological reduction in a number of aspects. The few specimens which have been collected from less restrictive habitats, such as drainage ditches, have much larger flowers and leaves. In southern Mexico and in South America, the plants attain greater size, although they still prefer such drier areas as savannas or forest margins. On the *llanos* of Argentina, the halophytic S. *gracile* again shows reduction.

Sarcostemma clausum has the widest range of the species in this subgenus, extending from Sonora and Florida to northern Argentina. It has developed numerous local variants of pubescence, leaf shape, and peduncle length, which have not been recognized taxonomically. It is unfortunate that the paucity of specimens from South America does not permit a detailed analysis of this interesting species.

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[51] Moore, Raymond J. Investigations on rubber-bearing plants. III. Development of normal and aborting seeds in *Asclepias syriaca* L. Can. Jour. Res. 24C:64. 1946.

[52] Meyer, T. Los generos "Funastrum" y "Philibertia." Lilloa 9:430. 1943.

[53] Hildebrand, F. Über die Entwicklung der haarigen Anhänge an Pflanzensamen. Bot. Zeit. 30:233, 257. 1872.

The species of the subgenus OXYSTELMA are divided among three sections, one of which is limited to the Old World. In the New World, the species of § PHILIBERTIA and § PENTACYPHUS occur in Andean South America, being centered, with respect to diversity, in northern Argentina and adjacent Bolivia. Like the species of subg. CERAMANTHUS in preferring more or less arid habitats, the American oxystelmas occur at moderate to high altitudes.

The single Old World species of subg. OXYSTELMA is *Sarcostemma* (§ EUOXYSTELMA) *esculentum*, which is a weedy plant ranging from Egypt through India to the islands of the East Indies. Apparently it grows in forest clearings and margins, especially along water courses. Its distribution possibly has been affected by man, for it occasionally is cultivated for its fruit and often is found in flower gardens because of its striking flowers.

The leafless sarcostemmas of subg. EUSARCOSTEMMA range from southernmost Africa and Madagascar, up the eastern coast of Africa to India, the East Indies, and Australia. They are plants of very dry, rocky or sandy areas, and their adaptation to these xeric habitats is manifest in the scale-like leaves and succulent, photosynthetic stems.

There are thus four main groupings of the species of *Sarcostemma*, which coincide in part with and substantiate the natural subgeneric groups recognized here. They suggest, also, that the genus itself is, in a sense, unnatural in that it includes several distinct evolutionary entities. This idea will be discussed further in the section on relationships. These major geographic and systematic groups include, then, the predominantly Mexican and Central American subg. CERAMANTHUS, the Andean subg. OXYSTELMA, § PHILIBERTIA and § PENTACYPHUS, and the two superposed Afro-Asian subg. OXYSTELMA, § EUOXYSTELMA and subg. EUSARCOSTEMMA (which do not appear to be closely related).

Although the systematics of the Old World forms is confused thoroughly at the specific level, it is possible to make certain comparisons between the subgenera and sections with respect to the number of species and degree of specialization and endemism which is apparent in each.

The subgenus CERAMANTHUS is the largest group, comprising fourteen closely related species which have been arranged taxonomically only in morphological series. Of these species, one is widespread, ten are of moderate extension, and three are rather strict endemics. Nearly all but the endemic species show one or several infraspecific groups at various levels of differentiation.

In the subgenus OXYSTELMA, there are nine species which break apart sharply into sections. In the Western Hemisphere, § PHILIBERTIA comprises five species which are fairly localized in their distribution; one species, however, is endemic to a small area in Argentina; another extends from southern Bolivia to south-central Argentina. About half of these species have developed infraspecific variants. The two species of § PENTACYPHUS are very distinct morphologically; again, one is rare, the other of moderate range.

Sarcostemma (§ EUOXYSTELMA) *esculentum* appears to be rather homogeneous throughout its range, differing only in vegetative characters and details of the fruit, and showing no tendency toward the striking floral variation of the New World forms. In this sense, it is comparable to *S.* (CERAMANTHUS) *clausum*, although it is the only species in the section and is very complex florally.

While it cannot be stated exactly to what degree the species of subg. EUSARCOSTEMMA are localized, it would appear that most have relatively wide distributions. Yet these species again seem to be very much alike in floral structure across their distribution from Africa to Asia.

These differences in degree of homogeneity and restriction to particular areas are rather interesting. They suggest that, of the three subgenera, CERAMANTHUS is undergoing the most rapid evolution at present. Subgenus OXYSTELMA appears to have achieved greater stability in certain respects, but in the New World is still becoming more diversified. On the other hand, the rather meagre evidence from the Old World seems to indicate that the species there are not actively developing new forms or are specializing along different lines.

RELATIONSHIPS

It has been mentioned that the taxonomy of the Asclepiadaceae is in a very confused state. Until a general system has been developed for the family, discussions of relationships and phylogeny scarcely will be intelligible. At present, the family is split into the Cynanchoideae, comprising the typical Asclepiadaceae with pollinia, and the much smaller, exclusively Old World, Periplocoideae, in which true pollinia are lacking. These divisions are discontinuous and undoubtedly natural, but the smaller subdivisions are less satisfactory.

The Cynanchoideae have been divided into four tribes: Asclepiadeae, Secamoneae, Tylophoreae, and Gonolobeae.[54] The Secamoneae, which have 4-locular anthers and occur only in the Old World, need not concern us. Woodson[55], after critical study of the other three tribes in North America, has presented a key to the tribes, the novel feature of which is his use of the sculptured, partially sterile pollinia of the Gonolobeae as a major character. The Asclepiadeae and Tylophoreae are distinguished, as is customary, by the position of the pollinia, i. e. whether pendulous or erect, respectively. Although the Gonolobeae have been defined unmistakeably, the distinction between the two tribes with uniformly fertile (with but rare exceptions), unsculptured pollinia seems not yet sufficiently decisive.

Sarcostemma is referred to the tribe Asclepiadeae of the Cynanchoideae. Since the genera which have been placed in synonymy have been drawn from three of Schumann's subtribes, no attempt will be made to allocate the genus to one of his artificial subdivisions. For the present, it must suffice to point out the morphological relationships of the genus.

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[54] Schumann, op. cit. 1897.
[55] Woodson, op. cit. 1941.

Sarcostemma is closest to *Cynanchum* and *Blepharodon*. The coronal appendages of *Cynanchum* usually are laminate and variously lobed or united. There are species, however, in which the corona lobes in life are quite fleshy so that little modification need be imagined to produce an inflated structure comparable to that of *Sarcostemma*. In those forms, however, the anther wings usually are not turned at an angle to the plane of the anther, nor are the pollen sacs usually apparent on the back of the anthers, as is characteristic of *Sarcostemma*.

The genus *Blepharodon* consists of two groups of species. Those typified by *B. nitidus* have corona segments which may be considered to consist of two radially arranged, laminate lobes partially fused by their margins. The second group, of which *B. mucronatum* is an example, has semi-vesicular corona segments which are open apically or closed by a thin membrane. In detail they are similar to those of the first group. Thus, from the standpoint of the corona, *Blepharodon* might be considered more or less transitional between *Cynanchum* and *Sarcostemma*. From the latter it differs in the saccate or vesicular corona segments, the anther wings usually in the same plane as the anther, and the very short caudicles bearing pyramidal pollinium-sacs. These same characters, however, together with details of the androecium and stigma-head, preclude relating the genera in linear sequence. Neither *Cynanchum* nor *Blepharodon* has a corona ring, though occasionally there are structures in each which might be mistaken for such.

I am not yet able to discuss satisfactorily the evolutionary relationships of the species of *Sarcostemma*, except for the statements made in connection with the section on geographical distribution and the discussion of certain minor trends which will be noted under the individual species. The plants apparently all have evolved toward the xerophytic type, for the most complex florally are the most specialized in this respect. In most cases the species have developed mechanical isolating mechanisms based on floral structure. Reasoning by analogy with the Asclepiadaceae which have been studied cytologically, it does not seem likely that polyploidy has played a significant role in the evolution of the genus.

I believe that the three subgenera and several sections recognized here are reasonably natural groups encompassing closely related species. Their aggregation into a broadly inclusive and arbitrary genus perhaps needs some explanation. While it may be our ideal to have a taxonomic system which expresses precisely the phylogeny of the organisms involved, the facts of evolution all too often do not permit this. Thus while species in the Asclepiadaceae generally are very well-marked, genera are extremely difficult to delimit. When the entire range of variation is considered, certain centers of variation can be perceived, and it would seem that these should be the basis for building up of genera by accretion, as it were. This has not been done, however, and the description of many small, ill-correlated genera has created a chaotic situation. Because of the nature of taxonomy and nomenclature, the only remedy is the establishment of inclusive, even if somewhat arbitrary, genera which will integrate these smaller groups into a usable system.

Materials

Specimens from the herbaria of the following institutions have been studied:

Chicago Museum of Natural History.
Dudley Herbarium of Stanford University.
Gray Herbarium of Harvard University.
University of Cambridge.
Missouri Botanical Garden.
Museum National de l'Histoire Naturelle, Paris.
Naturhistoriska Riksmuseet, Stockholm.
New York Botanical Garden.
Royal Botanic Gardens, Kew.
United States National Herbarium.
University of California, Berkeley.

I am indebted to the curators of these herbaria for the loan of this material, including many valuable types. I also wish to thank the staff of the Missouri Botanical Garden and its director, Dr. G. T. Moore, for the use of the library and herbarium facilities. To Dr. R. E. Woodson, Jr., I am especially grateful for his generous advice and invaluable constructive criticism.

For species in the United States, only one specimen per county has been cited. For those in other countries, nearly complete citations have been given. Data on habitat and blooming and fruiting time are summarized in the discussion following the description. The distribution maps include all specimens examined which could be located precisely. However, a complete list of all the plants examined is provided in the Index to Exsiccatae, together with the number of the species to which they are referred in this account.

Taxonomy

SARCOSTEMMA R. Brown, in Mem. Wern. Soc. 1:50. 1809, emend. R. Holm.

Oxystelma R. Br. loc. cit. 40. 1809.
Philibertia HBK. Nov. Gen. et Sp. Pl. 3:195. 1819.
Pentagonium Schauer, in Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1:364. 1843.
Lugonia Wedd. Chlor. And. 2:49. 1857.
Zosima Phil. Sert. Mend. Alt. 29. 1871, non Hoffm.
Funastrum Fourn. in Ann. Sci. Nat. Bot. VI, 14:388. 1882.
Cystostemma Fourn. in Mart. Fl. Bras. 6^4:204. 1885.
Philibertella Vail, in Bull. Torr. Bot. Club 24:305. 1897.
Ceramanthus (Kunze) Malme, in Ark. Bot. 4^{14}:2. 1905, nec Hassk. nec Hook. f. (based on *Sarcostemma* subg. CERAMANTHUS Kunze in Linnaea 20:26. 1847.)
Pentacyphus Schltr. in Engl. Bot. Jahrb. 37:605. 1906.
Tetraphysa Schltr. loc. cit. 616. 1906.

Suffrutescent, dextrorsely twining or trailing vines, rarely semi-erect, the stem variously little- or much-branched. Leaves usually laminate, sometimes reduced to scales, usually with one or more glands on the ventral surface of the midrib at the base; stipules minute. Inflorescences extra-axillary, cymose, racemiform to umbelliform, 1- to 30-flowered; peduncle present or absent. Calyx 5-lobed nearly to

the base which is adnate to the corolla, usually with 1 to many alternate or indefinitely distributed squamellae within. Corolla 5-lobed, rotate-subcampanulate, campanulate, or salverform. Stamens 5, the filaments coherent to form a column (rarely obsolete), usually produced at their insertion upon the corolla to form a patelliform corona ring often completely adnate to the corolla or to the filaments directly below the anthers, each filament bearing an inflated, vesicular segment (corona vesicle) directly below the anther; anthers 2-celled, the thecae apparent dorsally, the alae usually at 45° to the anther, the membranous dorsal appendage ovate to deltoid; pollinium-sacs oblongoid-cylindrical to clavate, nearly uniformly rounded or flattened, uniformly fertile (rarely with a small sterile region at the attachment of the caudicle), the corpusculum sagittate to ellipsoid, the slender caudicles exceeding the corpusculum in length, rarely very short. Carpels 2, somewhat subinferior, free towards the base, prolonged above into relatively conspicuous styles which unite to form a convex to 2-apiculate stigma-head. Follicle fusiform to obclavate; seeds unequally biconvex or flattened, with a micropylar coma.

Type species: *Sarcostemma viminale* (L.) R. Br.

KEY TO THE SUBGENERA

A. Stems never succulent; leaves laminate; inflorescence racemiform to umbelliform, the peduncle usually manifest; corolla rotate-subcampanulate, campanulate, or salverform; vesicles of the corona ovoid or obovoid to oblongoid or spheriod, ring of the corona free or adnate to the column directly below the anthers.

B. Corolla rotate-subcampanulate or salverform; ring of the corona free from the corolla, porrect (lacking in *S. flavum*); inflorescence corymbiform to umbelliform, 4- to 30-flowered. Species of the Western Hemisphere ..... Subgenus I. CERAMANTHUS (p. 506)

BB. Corolla campanulate; ring of the corona adnate to the corolla or more or less obsolete; inflorescence racemiform or umbelliform, 1- to 10-flowered. Species of the Eastern and Western Hemispheres. ..... Subgenus II. OXYSTELMA (p. 537)

AA. Stems succulent, or woody below; leaves scale-like throughout; inflorescence subumbelliform, the peduncle obsolete; corolla rotate-subcampanulate; vesicles of the corona ovoid, ring of the corona adnate to the filaments. Species of the Eastern Hemisphere..... Subgenus III. EUSARCOSTEMMA (p. 482)

Subgenus I. CERAMANTHUS Kunze, in Linnaea 20:26. 1847.

Philibertia acc. to Benth. in Benth. & Hook. Gen. Pl. 2:733. 1876, non HBK.
Funastrum Fourn. in Ann. Sci. Nat. Bot. VI, 14:388. 1882.
Cystostemma Fourn. in Mart. Fl. Bras. 6^4:204. 1885.
Philibertella Vail, in Bull. Torr. Bot. Club 24:305. 1897.
Ceramanthus (Kunze) Malme, in Ark. Bot. 4^{14}:2. 1905, nec Hassk. nec Hook. f.

Leaves laminate, rarely caducous or reduced; inflorescence corymbiform to umbelliform; corolla rotate-subcampanulate or salverform; ring of the corona usually pronounced (lacking in *S. flavum*).

Type species: *Sarcostemma elegans* Decne.

A closely knit group of species inhabiting drier regions of tropical and temperate America. The keys have been written so that flowers need not be studied critically for identification. Examination of the dried flowers with a hand lens often will provide a reassuring check on vegetative characters, however. All the

species recognized here differ from one another in many aspects of floral structure, but these differences often are difficult to describe adequately. Recourse may be had to the drawings of the gynostegia which have been made to show a condition typical for each species.

KEY TO THE SERIES

A. Ring of the corona present. Plants of North and South America.
  B. Inflorescence lateral to the main axis or lateral branch.
    C. Inflorescence corymbiform, obviously compound, the peduncle not equalling the subjacent internode in thickness; leaves usually densely white-tomentose beneath. Plants of Mexico.....Series 1. PANNOSA (Sp. 1)
    CC. Inflorescence umbelliform, the pedicels all inserted at nearly the same point; leaves never densely white-tomentose beneath.
      D. Peduncle equalling or exceeding the subjacent internode in thickness or lacking (when lacking, leaves obtuse to cuneate at the base), frequently bearing two catenulate cymes.....Series 2. CLAUSA (Spp. 2–3)
      DD. Peduncle not equalling the subjacent internode in thickness, or lacking (when lacking, leaves cordate), usually bearing but one cyme. .....Series 3. CYNANCHOIDES (Spp. 4–12)
  BB. Inflorescence terminal to the main axis or lateral branch, the peduncle not equalling the subjacent internode in thickness, or lacking. Plants of the Galapagos Islands.....Series 4. ANGUSTISSIMA (Sp. 13)
AA. Ring of the corona lacking. Plants of Argentina, Brazil and Uruguay. .....Series 5. FLAVA (Sp. 14)

Series 1. PANNOSA R. Holm, ser. nov.

Inflorescentia ut videtur lateralis corymbiformis certe composita, pedunculo quam internodio subjacenti angustiore.

Type species: *Sarcostemma pannosum* Decne.

A monotypic series which contains the presumably primitive species of the subgenus. The obviously compound inflorescence characterizes the series.

1. SARCOSTEMMA PANNOSUM Decne. in DC. Prodr. 8:540. 1844.

Sarcostemma rotundifolium Decne. loc. cit. 1844, ex char. (T.: *Mairet de la Chaux de Fond in Herb. DC.*).
Philibertia pannosa (Decne.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:320. 1881.
Philibertia rotundifolia (Decne.) Hemsl. loc. cit. 1881.
Philibertia Pavoni Hemsl. loc. cit. 319. 1881. (T.: *Ghiesbreght 200 in Herb. Kew.*!).
Philibertia tomentella T. S. Brandeg. in Univ. Calif. Publ. Bot. 4:90. 1900. (T.: *Brandegee 361 in Herb. Univ. Calif.*!).
Funastrum pannosum (Decne.) Schltr. in Fedde's Repert. 13:286. 1915.
Funastrum rotundifolium (Decne.) Schltr. loc. cit. 287. 1915.
Funastrum Pavoni (Hemsl.) Schltr. loc. cit. 286. 1915.
Funastrum tomentellum (Brandeg.) Schltr. loc. cit. 287. 1915.
Sarcostemma tomentellum (Brandeg.) Woods. in Ann. Mo. Bot. Gard. 28:217. 1941.

Stems twining, minutely pilosulose; lateral branches normally several. Leaves oblanceolate to obovate-elliptic, acuminate to mucronate, broadly and more or less obscurely cordate, 3.5–9.0 cm. long, 1.5–5.0 cm. wide, subcoriaceous, pilosulose above, densely white-tomentose beneath, with one or more glands on the midrib at the base; petiole 1–3 cm. long. Inflorescences corymbiform, 9- to 30-flowered; peduncle 3–7 cm. long, not equalling the subjacent internode in thickness, minutely pilosulose; bracts linear, minute; pedicels 2.0–3.5 cm. long, minutely pilosulose.

Calyx lobes narrowly ovate, 2.5–4.0 mm. long, pilosulose on both surfaces; squamellae absent or solitary. Corolla rotate-subcampanulate, white or cream-colored, the tube 1.5 mm. long, the lobes ovate, acuminate, 7–10 mm. long, pilosulose without, more or less puberulous-papillate within. Gynostegium 4 mm. high, the column 1.5 mm. long. Anthers 2 mm. long, the apical appendage ovate-suborbicular, the pollinium-sacs oblongoid-cylindrical, 1.2 mm. long with sagittate corpusculum; ring of the corona thin, revolute; vesicles of the corona obovoid, 2.5 mm. long. Ovaries 2.5 mm. long, the styles sericeous; stigma-head conical, 2-apiculate. Follicles broadly fusiform-obclavate, 5–7 cm. long, 2.0–2.5 cm. thick, puberulent; seeds unequally biconvex, 2.5–3.0 mm. long, 1.5–2.0 mm. wide, rufescent, rugose dorsally, papillate ventrally; coma about 2 cm. long.

An attractive species, well-marked by the white tomentum on the under-side of the leaf. In the very rare instances when this pubescence is not dense, the inflated follicle and compounding of the inflorescence are diagnostic. At least one segregate species has been based on a lack of undulation of the leaves *(P. Pavoni)*. However, I have found that on a single plant of *S. pannosum* in cultivation, the leaves may be plane or undulate. A similar situation obtains in *S. crispum*.

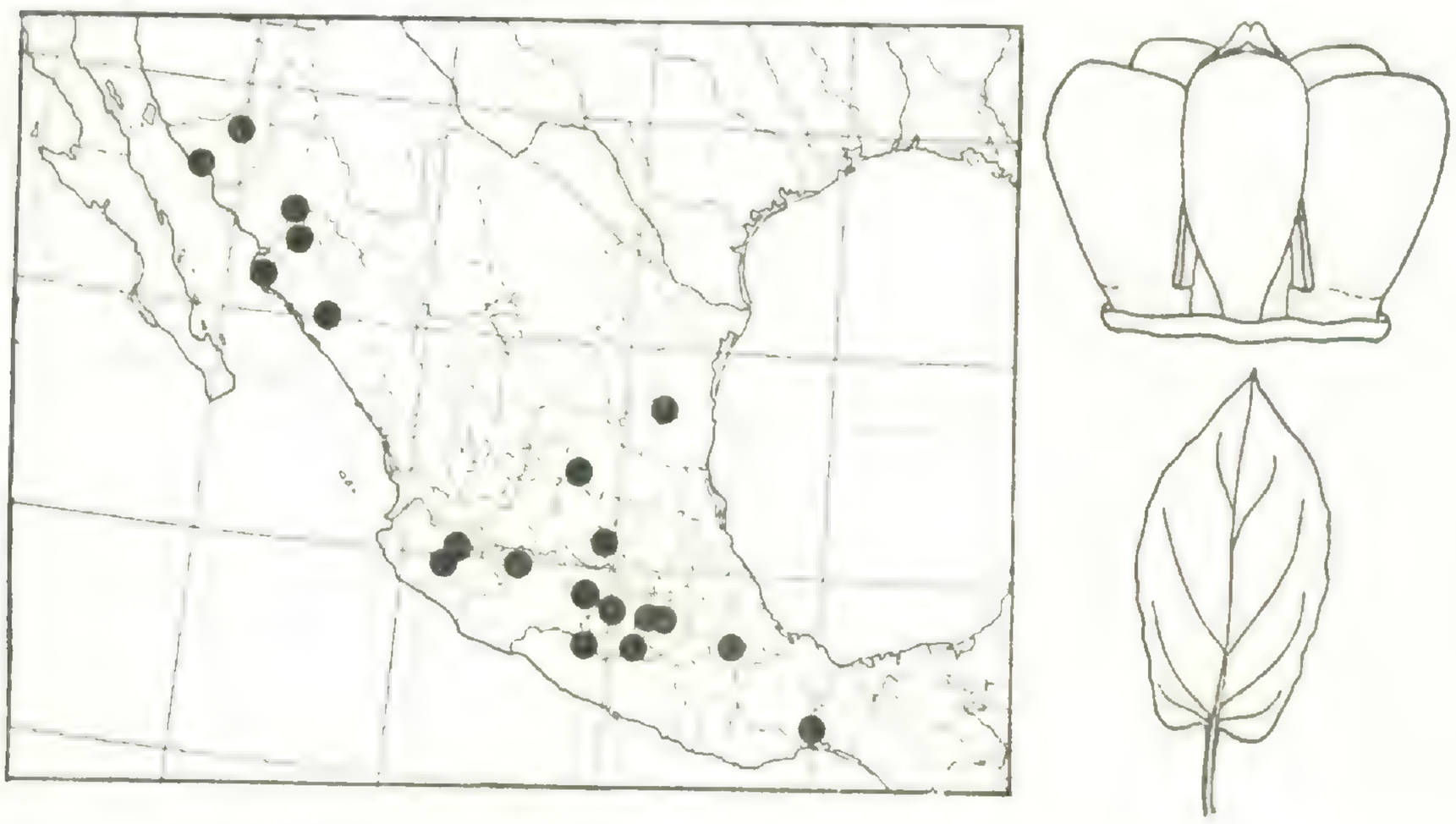

Fig. 5. Distribution, gynostegium, and leaf of *S. pannosum*.

Sarcostemma pannosum is endemic to Mexico, where it grows on grassy or rocky slopes from 500 to 6000 feet. It has been collected in flower from July 17 to November 19; fruit has been found from September 22 to November 13.

MEXICO. CHIHUAHUA: Guasarémos, Rio Mayo, *Gentry 2369*. DURANGO: loc. unknown, *Rose 2310*. GUERRERO: Pungarabato, Cayuca, *Hinton 6470*; Sierra Madre del Sur, Adama, Temisco, *Mexia 8861*; Placeres, Mina, *Hinton 10528*; Puerta de Oro, Mina, *Hinton 9175*; mts. near Iguala, *Pringle 13593*. JALISCO: Tuxcacuesco, *E. Anderson s. n.*; Rio Blanco, *E. Palmer 340*; Sacoaco, *M. E. Jones 319*. MEXICO: Temascáltepec, Vigas, *Hinton 1191*. MICHOACÁN: Monteleón, *Pringle 11028*; near Zamora, *Schery 182*; Tuzantla, Tiquicheo, Zitácuaro, *Hinton 13077*. MORELOS: near Yuatepec, *Rose, Painter & Rose 8585*; Cuernavaca, *Kenoyer C220, M. Martinez 150/02*. NAYARIT: Tepic, Los Bules,

Goldsmith 170. OAXACA: San Gerónimo, *Purpus 7180;* Oacalco, *Nagel 8086.* PUEBLA: Coxcatlán, *Purpus 4118.* QUERÉTARO: loc. unknown, *Agniel 14;* near Querétaro, *Rose & Rose 11152;* Querétaro, *Kuntze 23448.* SAN LUIS POTOSÍ: Las Canoas, *Pringle 3227.* SINALOA: Culiacán, *E. Palmer 1492;* El Brasíl, Rancho Tasajera, Choix, *Montes & Salazar 881;* Topolobambo, *E. Palmer 185;* near Labradas, *Ferris & Mexia 5247.* SONORA: 9 miles NE of Colorado, between Colorado & Mazatlán, *Wiggins & Rollins 328;* Guaymas, *E. Palmer 195.* TAMAULIPAS: near Victoria, *Palmer 497.*

Series 2. CLAUSA R. Holm, ser. nov.

Inflorescentia ut videtur lateralis umbelliformis saepe cymis catenulatis duobus, pedunculo internodium subjacens crassitudine aequante vel excedente (interdum obsoleto).

Type species: *Sarcostemma clausum* (Jacq.) R. & S.

This series includes two species which share the character of having peduncles as thick as, or thicker than the subjacent internode. It is also quite common to find two umbelliform clusters of flowers upon the same peduncle, one terminal, the other lateral.

KEY TO THE SPECIES

a. Corolla salverform, the tube definitely constricted; ovaries glabrous throughout; plants more or less glaucous throughout..... 2. *S. glaucum*

aa. Corolla rotate-subcampanulate, the tube not definitely constricted; ovaries sericeous throughout or with densely sericeous styles; plants glabrescent to sericeous..... 3. *S. clausum*

2. SARCOSTEMMA GLAUCUM HBK. Nov. Gen. et Sp. Pl. 3:194. 1819, ex char.

(T.: *Humboldt & Bonpland s. n. in Herb. Paris.*).

Funastrum glaucum (HBK). Schltr. in Fedde's Repert. 13:285. 1915.
Philibertella ovalifolia Rusby, Descr. So. Am. Pl. 94. 1915. (T.: *H. H. Smith 1683 in Herb. N. Y. Bot. Gard.*!).
Funastrum ovalifolium (Rusby) Killip, in Jour. Wash. Acad. Sci. 21:351. 1931.

Stems twining, gray-green, glabrous; lateral branches normally few. Leaves narrowly elliptic, oblong to ovate, acute, cuneate to obtuse, 5.0–7.5 cm. long, 0.5–3.0 cm. wide, subcoriaceous, revolute when dried, glaucous, glabrous on both surfaces, with one or more glands on the midrib at the base; petiole 0.3–0.5 cm. long. Inflorescences umbelliform, 18- to 35-flowered; peduncle 0–7 cm. long, equalling the subjacent internode in thickness, often bearing two catenulate cymes, glabrous; bracts linear, minute; pedicels 1–2 cm. long, glabrous. Calyx lobes ovate, 1.5 mm. long, glabrate on both surfaces, ciliolate; squamellae absent. Corolla salverform, white, the tube 2 mm. long, constricted, the lobes ovate, obtuse, 4–6 mm. long, puberulous-papillate on both surfaces, ciliolate. Gynostegium 2 mm. high, the column about 0.5–1.0 mm. long. Anthers 1.5 mm. long, the apical appendage deltoid, the pollinium-sacs oblongoid, somewhat flattened, 0.75 mm. long, with ellipsoid-sagittate corpusculum; ring of the corona prominent, revolute, adnate to the base of the corona vesicles; vesicles of the corona ovoid, pointed at the tip, 1.5–2.0 mm. long. Ovaries 3 mm. long, glabrous; stigma-head conical, obscurely 2-fid. Follicles narrowly obclavate-fusiform, 8.5 cm. long, 1 cm. thick,

glabrous; seeds flattened, 6 mm. long, 4 mm. wide, minutely papillate on both surfaces, the margin thin and serrate apically; coma about 2.5 cm. long.

This species often is confused with S. *clausum*, but although the two are alike superficially, there are a number of characters to separate them. One of the best is the fact that the corolla tube is constricted in S. *glaucum*, while the flowers are somewhat smaller and more abundantly produced. As the specific name suggests, S. *glaucum* has a characteristic glaucous aspect throughout. The doubled inflorescence also is more common in this species, where the peduncle sometimes is absent.

Philibertella ovalifolia Rusby was described for a variant with leaves wider than those of the typical form, but the two sorts occur in the same area and merge with one another. Although S. *glaucum* appears to be fairly common, only one specimen with fruit has been seen.

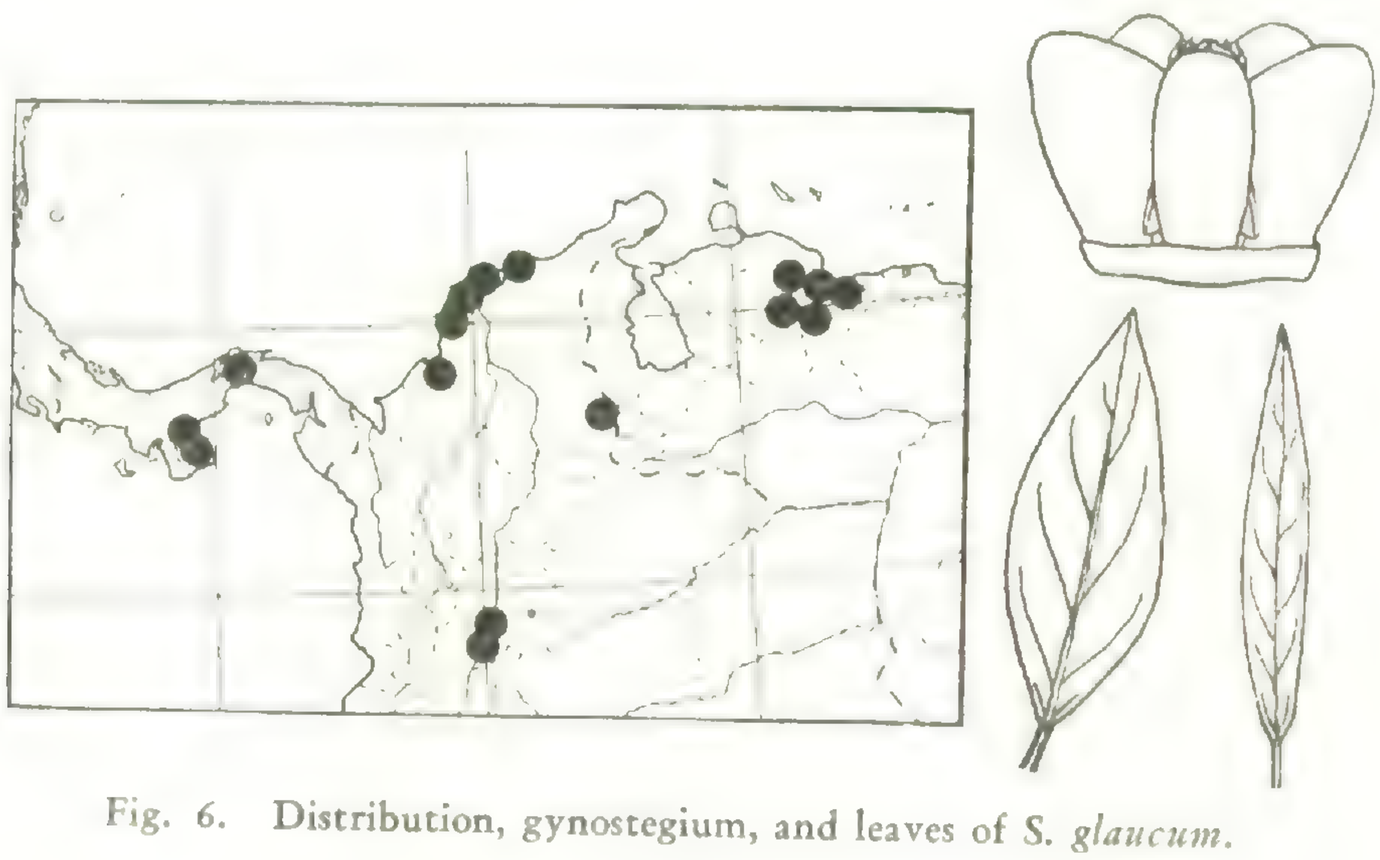

Fig. 6. Distribution, gynostegium, and leaves of S. *glaucum*.

Sarcostemma glaucum has been collected in Panama, Venezuela, and Colombia, where it grows along the coast, both in marshy and arid thickets or forest margins. The maximum recorded altitude attained by the species is 2500 feet, but it appears to be more common near sea level. Flowering specimens are dated from July 19 to March 6.

PANAMA. COCLÉ: Aguadulce, *Pittier 4977*. HERRERA: near Chitré, *Allen 1090*. PANAMA: Juan Díaz, *Standley 30510*.

COLOMBIA. ATLÁNTICO: Ponedera, *Dugand & Jaramillo 2750;* between Palmar de Varela & Pondedera, *Dugand 3658;* Puerto Giraldo, *Dugand & Jaramillo 4187*. BOLIVAR: Cartagena, *E. Martínez 83, Heriberto 288;* Barranquilla, *Elias 441, Dugand 102;* Los Volcánes, near Turbaco, *Killip & Smith 21111, 14323;* S of Mawatoca, *H. H. Smith 2779;* Sincelejo, *Pennell 4058*. CUNDINAMARCA: Girardot, *Rusby & Pennell 76;* Hacienda El Cucharo, between Tocaima & Pubenza, *Killip, Dugand & Jaramillo 38922*. HUILA: quebrada de Ángeles to Río Cabrera, *Rusby & Pennell 342*. MAGDALENA: Santa Marta, *H. H. Smith 1682, 2524, Killip & Smith 21105*. SANTANDER DEL NORTE: Cúcuta, *Killip & Smith 20999*.

VENEZUELA. ARAGUA: La Trinidad de Maracay, *Pittier 5783*. CARABOBO: near Valencia, *Pittier 9429;* near Trincheras, near Valencia, *Pittier 7653*. LARA: Barquisimeto, *Santiago 60*. PORTUGUESA: near Acarigua, *L. Williams 12460*. ZULIA: near Perijá, *Tejera 201, 225*.

PERU. data incomplete, *Maclean s. n.*

3. SARCOSTEMMA CLAUSUM (Jacq.) Roem. & Schult. Syst. Veg. 6:116. 1820.

Cynanchum clausum Jacq. Select. Stirp. Amer. 1:87, *t. 60.* 1763.
Asclepias viminalis Sw. Prodr. 53. 1788.
Sarcostemma Brownei G. F. Meyer, Prim. Fl. Esseq. 139. 1818.
Sarcostemma cumanense HBK. Nov. Gen. et Sp. Pl. 3:195. 1819, ex char. (T.: *Humboldt & Bonpland s. n. in Herb. Paris.*).
Sarcostemma pubescens HBK. loc. cit. 194. 1819, ex char. (T.: *Humboldt & Bonpland s. n. in Herb. Paris.*).
Sarcostemma Swartzianum Schult. Syst. Veg. 6:116. 1820.
Sarcostemma lineare Spreng. Neue Entd. 3:35. 1822, non Decne.
Sarcostemma bonariense Hook. & Arn. in Hook. Lond. Jour. Bot. 1:296. 1834, ex char. (T.: *Tweedie s. n. in Herb. Kew.*).
Sarcostemma apiculatum Decne. in DC. Prodr. 8:539. 1844, ex char. (T.: *Gardner 819 in Herb. Delessert*).
Sarcostemma crassifolium Decne. loc. cit. 540. 1844, ex char. (T.: *Galeotti 1529 in Herb. Paris.*).
Sarcostemma Dombeyanum Decne. loc. cit. 539. 1844. (T.: *Dombey s.n. in Herb. Paris*!).
Sarcostemma riparium Decne. loc. cit. 540. 1844, ex char. (T.: *in Herb. Paris.*).
Philibertia viminalis (Sw.) A. Gray, in Proc. Amer. Acad. 12:64. 1877.
Philibertia crassifolia (Decne.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:318. 1881.
Philibertia cumanensis (HBK.) Hemsl. loc. cit. 1881.
Sarcostemma barbatum Mart. ex Fourn. in Mart. Fl. Bras. 6^4:235. 1885, ex char. (T.: *Martius s. n.*).
Sarcostemma bifidum Fourn. loc. cit. 234. 1885, ex char. (T.: *Mikan I in Herb. Vindobon.*).
Sarcostemma cuspidatum Fourn. loc. cit. 233. 1885, ex char. (T.: *Poeppig 2923 in Herb. Vindobon.*).
Sarcostemma Gardneri Fourn. loc. cit. 1885, ex char. (T.: *Gardner 1357*).
Sarcostemma pallidum Fourn. loc. cit. 235. 1885, ex char. (T.: *St. Hilaire Cat. C^2 1489*).
Sarcostemma pedunculatum Fourn. loc. cit. 1885, ex char. (T.: *Glaziou 8168 in Herb. Paris.*).
Sarcostemma Schottii Fourn. loc. cit. 234. 1885, ex char. (T.: *Pohl & Schott 5381 in Herb. Vindobon.*).
Philibertia Palmeri A. Gray, in Proc. Amer. Acad. 21:394. 1886. (T.: *Palmer 5 in Herb. Gray*!).
Philibertia clausa (Jacq.) K. Schum. in E. & P. Nat. Pflanzenfam. 4^2:229. 1895.
Philibertia Gardneri (Fourn.) K. Schum. loc. cit. 1895.
Philibertella clausa (Jacq.) Vail, in Bull. Torr. Bot. Club 24:306. 1897.
Philibertella crassifolia (Decne.) Vail, loc. cit. 1897.
Philibertella cumanensis (HBK.) Vail, loc. cit. 1897.
Philibertella Palmeri Vail, loc. cit. 1897.
Sarcostemma Glaziovii K. Schum. in Engl. Bot. Jahrb. 25, Beibl. 60:19. 1898, ex char. (T.: *Glaziou 21744 in Herb. Berol.*).
Philibertia bonariensis (H. & A.) Malme, in Sv. Vet. Akad. Afh. 34:23. 1900.
Philibertia cuspidata (Fourn.) Malme, loc cit. 24. 1900.
Philibertia riparia (Decne.) Malme, in Bih. Sv. Akad. Vet. 27:7. 1901.
Philibertella lasiantha Schltr. in Engl. Bot. Jahrb. 37:607. 1906, ex char. (T.: *Eggers 14547 in Herb. Berol.*).
Philibertella pallida (Fourn.) Schltr. loc. cit. 1906.
Philibertella pedunculata (Fourn.) Schltr. loc. cit. 1906.
Cynanchum mexicanum T. S. Brandeg. in Univ. Calif. Publ. Bot. 4:380. 1913. (T.: *Purpus 6017 in Herb. Univ. Calif.*!).
Philibertella riparia (Decne.) Stuntz, Invent., U. S. Bur. Pl. Ind. 31:87. 1914.
Funastrum apiculatum (Decne.) Schltr. in Fedde's Repert. 13:283. 1915.
Funastrum barbatum (Mart.) Schltr. loc. cit. 1915.

Funastrum bonariense (H. & A.) Schltr. loc. cit. 1915.
Funastrum clausum (Jacq.) Schltr. loc. cit. 1915.
Funastrum crassifolium (Decne.) Schltr. loc. cit. 1915.
Funastrum cumanense (HBK.) Schltr. loc. cit. 1915.
Funastrum cuspidatum (Fourn.) Schltr. loc. cit. 1915.
Funastrum Dombeyanum (Decne.) Schltr. loc. cit. 1915.
Funastrum Gardneri (Fourn.) Schltr. loc. cit. 1915.
Funastrum Glaziovii (K. Sch.) Schltr. loc. cit. 1915.
Funastrum lasianthum Schltr. loc. cit. 1915.
Funastrum pallidum (Fourn.) Schltr. loc. cit. 1915.
Funastrum Palmeri (A. Gray) Schltr. loc. cit. 1915.
Funastrum pedunculatum (Fourn.) Schltr. loc. cit. 1915.
Funastrum pubescens (HBK). Schltr. loc. cit. 1915.
Funastrum riparium (Decne.) Schltr. loc. cit. 1915.
Funastrum Schottii (Fourn.) Schltr. loc. cit. 287. 1915.
Funastrum fragile Rusby, in Mem. N. Y. Bot. Gard. 7:332. 1927. (T.: *White 2088 in Herb. N. Y. Bot. Gard.*!).
Funastrum lanceolatum Rusby, loc. cit. 1927. (T.: *M. Cardenas 2 in Herb. N. Y. Bot. Gard.*!).
Funastrum Seibertii Woods. in Ann. Mo. Bot. Gard. 24:199. 1937. (T.: *Seibert 637 in Herb. Mo. Bot. Gard.*!).

Stems twining or trailing, gray-green, glabrous, the nodes densely white-pubescent; lateral branches normally few. Leaves frequently caducous, elliptic to oval, rarely much reduced, acuminate to mucronate, obtuse to shallowly cordate, 2–5 cm. long, 0.5–2.5 cm. wide, membranaceous to subcoriaceous, glabrate to sericeous above and beneath, with one or more glands on the midrib at the base; petiole 0.2–0.6 cm. long. Inflorescences umbelliform, rarely with two catenulate cymes, 7- to 15-flowered; peduncle stout, usually equalling the subjacent internode in thickness, 3.5–6.0 cm. long, glabrate to sericeous; bracts linear, minute; pedicels 1.5–2.5 cm. long, glabrate to puberulent. Calyx lobes ovate, 3–4 mm. long, densely puberulent without, glabrate within; squamellae alternate, paired or solitary. Corolla rotate-subcampanulate, pale greenish yellow to white, the tube 2.5 mm. long, not definitely constricted, the lobes ovate-elliptic, acute, 6–9 mm. long, densely puberulent without, glabrate to minutely puberulent within, ciliolate. Gynostegium 3 mm. high, the column short, about 0.5 mm. long. Anthers 1.5 mm. long, the apical appendage reniform to orbicular, the pollinium-sacs cylindrical-oblongoid, 1.8 mm. long, with sagittate corpusculum; ring of the corona prominent, revolute, adnate to the base of the corona vesicles; vesicles of the corona ovoid, pointed at the tip, 2.5 mm. long. Ovaries 2.5 mm. long, the styles sericeous, rarely sericeous throughout; stigma-head convex, with a short 2-fid apiculation. Follicles obclavate, attenuate, 5.0–8.5 cm. long, 1.2–1.5 cm. thick, puberulent, finely striate; seeds flattened, 4–6 mm. long, 2–3 mm. wide, minutely papillate on both surfaces, the margin thin and serrate apically; coma about 2 cm. long.

A species as bewilderingly variable as *Sarcostemma clausum* poses a serious question for the taxonomist. Although sufficiently common and variable to have developed a phenomenal synonymy, it is not sufficiently abundant in herbaria for analyses of variation to be made. Undoubtedly a species which ranges from southern United States to Argentina, which occupies both hydric and xeric habitats, and

which is insect-pollinated, will differentiate ecologic or geographic populations. Only very limited samples, often of a single plant, of these local groups are available to the botanist. In such a case, one alternative is to describe each specimen which is different in several aspects of morphology as new, in the hope that it eventually will be found to be a valid species. This is what has been done in the past with the majority of the Asclepiadaceae. The other alternative is to recognize that the specimen is slightly different in one, or perhaps several characters, but to refrain from describing it as a species until it can be proven to be a well-defined population which has achieved some measure of isolation from its cogeners.

After studying the some few hundred specimens collected from the entire range of S. *clausum,* I have come to the conclusion that there are essentially no significant differences, although the leaves are quite variable in shape, size, and pubescence, and the peduncles vary in size and thickness. The fact that these vegetative forms tend to occupy certain regions indicates that S. *clausum* probably has differentiated into several subspecific groups. It would be extremely dangerous to attempt to define the limits of such intergrading populations on the basis of a very few examples. I have followed, therefore, the alternative of recognizing only one species which eventually will perhaps be split into smaller groups.

Sarcostemma clausum, generally speaking, inhabits less arid habitats than most of the species of the genus. In Florida, Central America, and eastern South

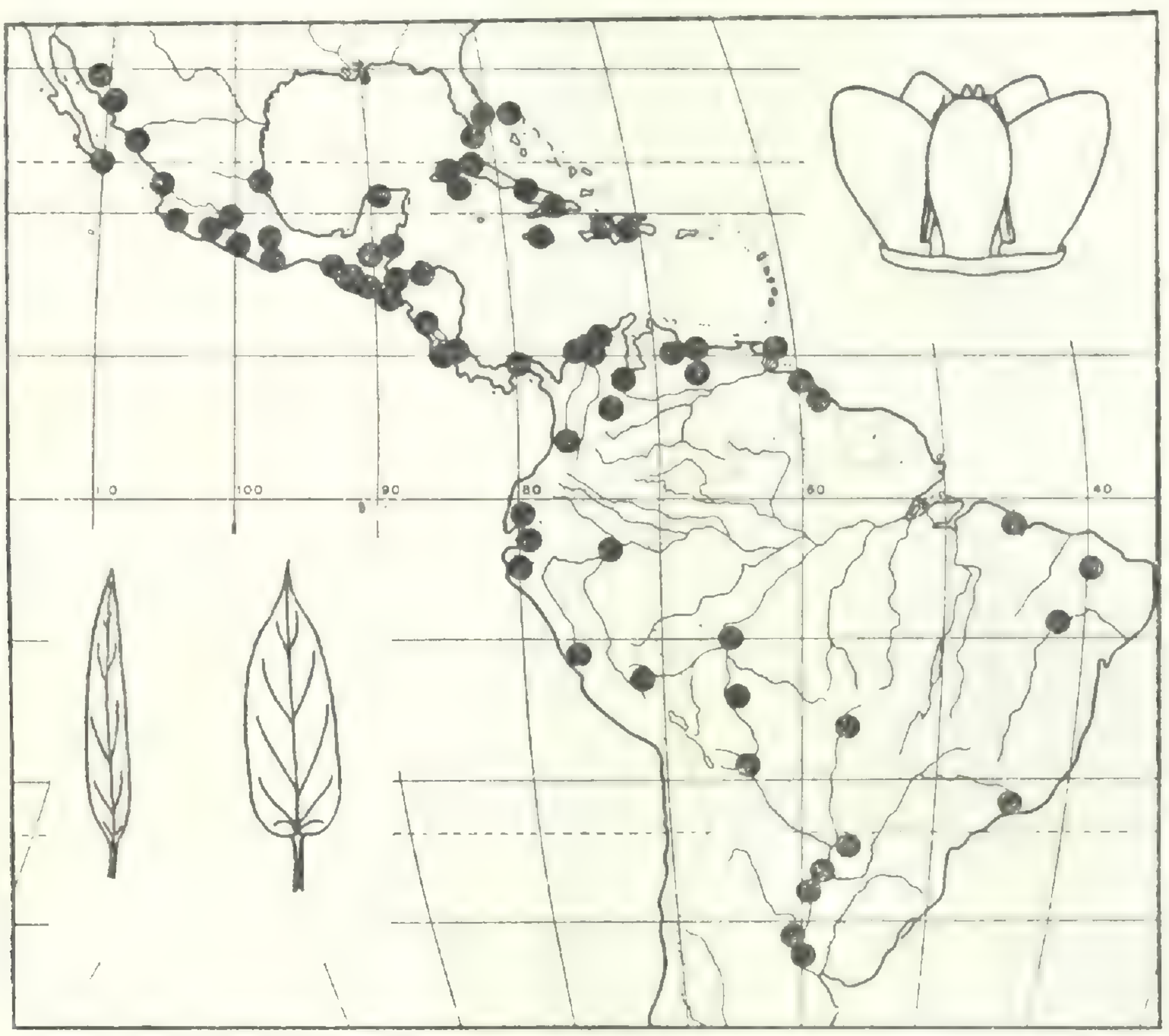

Fig. 7. Leaves, distribution, and gynostegium of S. *clausum*.

America, it is found on wooded slopes or in flood plains, or even growing in several feet of water. In Mexico and northwestern South America, on the other hand, it is commonest in sandy strand areas or savannas. The altitudinal range is from sea level to about 4000 feet. The plant apparently is in flower the year round through most of its range and has been described as "extremely fragrant, covered with masses of white flowers."

UNITED STATES. FLORIDA: DADE CO.: Miami, *Garber 11939*. LEE CO.: Fort Myers, *Hitchcock 207*. MONROE CO.: Fishbone Key, *Seibert 1337*; Big Pine Key, *Killip 3174*; Key West, *Curtiss 5624*; Bahia Honda Key, *Woodson & Schery 119*; Elliot's Key, *Small & Nash s. n.*

MEXICO. BAJA CALIFORNIA SUR: San José del Cabo, *T. S. Brandegee s. n.*; S of San José del Cabo, *Johansen 514*. CHIAPAS: Jalisco, *Purpus 0170*; Escuintla, *Matuda 0699*. CHIHUAHUA: SW Chihuahua, *E. Palmer 5*, type of *P. Palmeri* Gray. COLIMA: Manzanillo, *Ferris 6128*, *Palmer 1002*; Paso del Río, *Emrick 11*. GUERRERO: Baqueta, *Langlassé 508*; Guayameo, Mina, *Hinton 9370*; Actoyac, Galeana, *Hinton 14602*; Vallecitos, Montes de Oca, *Hinton 10607*; Pungarabato, Coyuca, *Hinton 6452*; NW of Acapulco, *Barkley 14103*. JALISCO: Bolaños, *Rose 2912*; Tenacatita Bay, *Elmore 1A23*. MICHOACAN: Coalcomán, Aquila, *Hinton 15833*. MORELOS: near Cuernavaca, *Pringle 7109*; Xochitepec, *Lyonnet 1037*. NAYARIT: Mexcaltitlán, *Mexia 1016*. OAXACA: near Tomellin, *Rose, Painter & Rose 10054*; near Cuicatlán, *E. W. Nelson 1615, 1680*, *L. C. Smith 240*; Chiltepec, Tuxtepec, *Martínez-Calderón 196*; San Antonio, *C. L. Smith 836*, *Pringle 4840*; Tomellin, *Olssen-Seffer s. n.*; Etla, near Bocas del Ríos, *Seler & Seler 4852*. SINALOA: Culiacán, *T. Brandegee s. n.*; loc. unknown, *Ortega 4230*. SONORA: Hermosillo, *Drouet & Richards 3564*; 23 miles NE Ures, *Shreve 6732*; Río Mayo, *Gentry 2286*; near Batuc, *Wiggins & Rollins 454*; 25 miles from Ures, *Wiggins 7387*. TABASCO: Caño de Curahue, *Rovirosa 32*. TAMAULIPAS: Tampico, *E. Palmer 408*. VERA CRUZ: Pánuco River near Ebano, *Le Sueur 358*; loc. unknown, *Purpus 6017*, type of *C. mexicanum* Brandeg. YUCATAN: Progreso, *Flores 7*.

BRITISH HONDURAS: Corozal District, *Gentle 503, 807*; Honey Camp, *Lundell 517*; Santa Rita, *Gentle 73*; Northern River, *Gentle 883*.

GUATEMALA. ALTA VERAPAZ: Samac, *Johnson 776*; Pancajche, *Johnson 1017*. AMATITLÁN: Amatitlán, *von Tuerckheim 8710*, *J. D. Smith 2778*, *Morales 1136*; Lake Amatitlán, *Kellerman 4350*, *J. D. Smith 1940*. CHIQUIMULA: near Chiquimula, *Standley 73865*. ESCUINTLA: Río Guacalate, *Standley 58204, 60163*; San José, *Standley 63061*, *Hayes s. n.* GUATEMALA: near Lago de Amatitlán, *Standley 89433*. JUTIAPA: near Jutiapa, *Standley 75185*. IZABAL: Boca del Palochi, *J. D. Smith 1734*; NE of San Felipe, *Steyermark 39662*. PETÉN: S of Sayaxche, *Steyermark 46220*. RETALHULEU: near Retalhuleu, *Standley 88251, 88837*. SAN MARCOS: Ocós, *Steyermark 37820*; Río Suchiate, W of Ayutla, *Steyermark 38030*. SOLOLA: S-facing slopes, Volcán Atitlán, *Steyermark 48010*; Santa Barbara, *Shannon 160*. SANTA ROSA: Ríos de los Esclavos, *Heyde & Lux 4001*; Casillos, *Aquilar 303*; Agua Caliente, *Kellerman 7737*. SUCHITEPEQUEZ: Río Najuala, *Shannon 309*. ZÁCAPA: Baños de Santa Marta, *Standley 73932*; Zácapa, *Deam 154*, *Kellerman 4350*.

EL SALVADOR. AHUACHAPÁN: loc. unknown, *Padilla 115*. SAN SALVADÓR: along road from San Martín to Laguna de Ilopango, *Standley 22589*.

HONDURAS. ATLÁNTIDA: Tela, *Standley 54664*. CORTES: Rio Lindo, *Edwards P-683*. SANTA BARBARA: San Pedro Sula, *Thieme 5342*. YORO: near Coyoles, Aguán Valley, *Yuncker, Koepper & Wagner 8122*.

NICARAGUA. GRANADA: Granada, *Grant 903*. MANAGUA: near Managua, *Garnier A128*.

COSTA RICA. SAN JOSÉ: near El Generál, *Skutch 2171*. TALAMANCA: Delta de Turitkub, *Tonduz 8661*.

PANAMA. BOCAS DEL TORO: Changuinola River, *Dunlap 289*. CANAL ZONE: Barro Colorado Island, *Bangham 413*, *Kenoyer 501*, *Shattuck 315, 1114*, *Brown 155*, *Wilson 66*, *Bailey & Bailey 530*; near Empire, Culebra Cut, *Hunter & Allen 775*. PANAMÁ: swamp

between El Jagua Hunting Club on Río Jagua and El Condor Hill, *Hunter & Allen 482;* near Arenoso, lower Río Trinidád, *Seibert 637.*

CUBA. CAMAGUEY: Cayo Romano, *Shafer 2494;* Cayo Sabinal, Granada, *Shafer 877.* HAVANA: Laguna de Castellano, *P. Wilson 9559;* San Antonio, *Shafer 247.* ORIENTE: Ensenada de Mora, *Britton, Cowell & Shafer 12960;* near Nirua-Nirua, *Britton & Cowell 12719;* Bayamo, *Ekman 7590;* Río Jagua, *Ekman 6653; Wright 1666.* ISLA DE PINOS: Nueva Gerona, *Curtiss s. n.;* Don José, *Blain 104.* LAS VILLAS: Belmonte, Sóledad, Cienfuegos, *Jack 7728, 6856, 5342;* Cienfuegos, Cienquita, *Combs 330;* Ciénaga de Zapata, N of Bahía de Cochinas, *Leon & Soustalot 8497;* Gavilon, vic. Sóledad, *Howard 6298.* PINAR DEL RÍO: near Mendoza, *Shafer 10608;* Laguna Jovera, *Shafer 10983.*

HISPANIOLA. HAITI: near Port au Prince, *Leonard 10092;* near Gros Morne, *Leonard 9934, 9980;* near Jean Rabel, *Leonard & Leonard 12799;* near Étang, *Leonard 3570.*

DOMINICAN REPUBLIC: Barahona, *Fuertes 202, 1260;* S of Monte Cristi, near Río Yaque del Norte, *Howard & Howard 9569.*

JAMAICA: Blue Mts., *Hitchcock s. n.;* Arntully, *Orcutt 3111;* Port Henderson, *Harris & Lawrence C1536;* Hope Bay, *Wight 169;* Kingston, *Brown 379;* below Cinchona, *Maxon & Killip 1043.*

BAHAMA ISLANDS: New Islands, *Britton & Brace 482, 770;* Great Bahama, *Brace 3602, Britton & Millspaugh 2661.*

TRINIDAD: east of Icacos, *Cheesman & Baker 388.*

COLOMBIA. AMAZONAS: Río Putamayo, between Río Igara-Paraná and Río Yaguas, *Schultes 3998.* BOLÍVAR: Calamar, *Killip & Smith 14708;* near Turbaco, *Killip & Smith 14437;* Buenavista, east of Sincé, *Pennell 3981;* near Puerto Colómbia, *Elias 396.* CAUCA: La Manuelita, Palmira, *Pittier 787.* EL VALLE: Espiñol, below Dagua, *Killip & Hazen 11076;* N of Palmire, *Garcia B. 6408;* "La Manuelita," *Pennell & Killip 6191.* HUILA: above Natagaima, *Rusby & Pennell 270.* MAGDALENA: Santa Marta, *H. H. Smith 1681;* Fonseca, *Haught 4387;* 15 miles N of Becerril, *Haught 3694.* SANTANDER: Puerto Wilches, *Killip & Smith 14937.* SANTANDER DEL NORTE: near Sarare, *Cuatrecasas 13258;* near Florida, *Killip & Smith 16176.* TOLIMA: Doima, *Haught 2442;* Mariquita, *Pennell 3632.*

ECUADOR. GUAYAS: Guayaquil, *Mille 961, Asplund 5150.* LOS RÍOS: Río Pita, *Asplund 5588.*

PERU. APURIMAC: Abancay, *Vargas 750.* LIMA: Hacienda Peramango, Río Pativilea Valley, *Seibert 2313;* Chosica, *Macbride & Featherstone 535.* LORETO: Iquitos, Creek Itaya, *Mexia 6482.* PIURA: Huancabamba, Serran, *Stork 11387;* Negritos, *Haught F-40;* Pariñas Valley, *Haught 145, Spruce 6486.* TUMBES: Tumbes, mts. SE Hacienda La Choza, *Weberbauer 7694.*

VENEZUELA. ARAGUA: Maracay, El Limón, *Pittier 10102;* potreros de Las Delicias, *Lasser 860.* DISTRITO FEDERAL: Bajo Cotiza, *Vogl 458;* near Caracas, *Eggers 13121, Pittier 7583.* GUARICO: El Sombrero, *Pittier 13557.* FALCON: Meachiche, *Lasser 186.* MÉRIDA: Tovar, *Fendler 1054.* YARACUY: near Guama, *Pittier 11163.*

BRITISH GUIANA: Vreed-en-Hoop, *Hitchcock 16738;* Morawhanna, *Hitchcock 17511;* Parika, *Hitchcock 16754;* east coast, *Persaud 302.*

SURINAM: *Hostmann 962.*

BRAZIL. CEARÁ: Carupe, *Drouet 2619;* Río de Janeiro, *Glaziou 8168, Dusén 1968.* MATTO GROSSO: Cuyabá, *Malme 3247, Hoehne 25072;* Santa Cruz de Parra, *Lindman A2853.* PARÁ: 2 km. S Baião, *Drouet 1992.* RIO DE JANEIRO: Isla Paqueta, *Dusén 5.*

BOLIVIA. SANTA CRUZ: Portachuelo, *Steinbach 3235;* W of Río Parai, *Herzog 1362;* Río Ibon, *O. E. White 2088,* type of *F. fragile* Rusby.

PARAGUAY: Asunción, *Morong 681, Malme s. n.;* Carapeguá, *Rojas 3220; Ypacaray, Hassler 72118;* Pilcomayo River, *Morong 1526;* Laguna Ypacaray, *Fiebrig 331, Hassler 12118;* Santa Elisa, *Hassler 2760;* between Río Apa and Río Aquidaban, *Fiebrig 4250.*

ARGENTINA. CHACO: Fontana, *T. Meyer 215;* La Fidelidad, *Jörgensen 3037.* FORMOSA: Formosa, *Jörgensen 1918, 2606;* Gubernación Formosa, *Kermes 380.* JUJUY: San Pedro de Jujuy, *Schreiter 5207.* SALTA: Orán, *Schreiter 33559, 10842;* Embaración, *Schreiter 5227.* SANTA FE: Los Amores, Generál Obligado, *Ragonese 3235.*

Series 3. CYNANCHOIDES R. Holm, ser. nov.

Inflorescentia ut videtur lateralis umbelliformis, cyma una, pedunculo quam internodio subjacenti angustiore (interdum obsoleto).

Type species: *Sarcostemma cynanchoides* Decne.

This largest series of the subgenus CERAMANTHUS includes those species which have lateral inflorescences borne upon peduncles not equalling the subjacent internode in thickness. They represent an apparently natural group which, however, is further divisible into groups of closely related species. These subdivisions have not been recognized nomenclaturally, but their relationships are discussed in connection with the particular species which they include, and are also expressed in the key.

KEY TO THE SPECIES

a. Leaves very broadly ovate-cordate to orbicular, the base cordate with converging lobes.
  b. Petals strongly reflexed at maturity; ring of the corona relatively long and conspicuous; column nearly equalling the corona vesicles in length; corona vesicles ovoid to pyramidal. Plants of Mexico, Central America, and northeastern South America ..... 4. *S. bilobum*
  bb. Petals not reflexed at maturity; ring of the corona relatively short; column nearly obsolete; corona vesicles ovoid; leaves long-mucronate, conspicuously paler beneath. Plants of Guatemala ..... 5. *S. odoratum*
aa. Leaves broadly to narrowly lanceolate, the base usually cordate with descending or diverging lobes, obtuse or cuneate in very narrow leaves.
  b. Petals strongly reflexed at maturity; leaves long, linear. Plants of South America ..... 6. *S. gracile*
  bb. Petals not strongly reflexed at maturity; leaves lanceolate to linear. Plants of North America.
    c. Column exceeding the corona vesicles in length; vesicles of the corona constricted at their insertion upon the column; leaves very long, narrowly lanceolate, the margin usually undulate-crispate; follicles very attenuate ..... 7. *S. crispum*
    cc. Column shorter than the corona vesicles; vesicles of the corona not constricted at their insertion upon the column; leaves lanceolate to linear, the margin not undulate-crispate.
      d. Corolla segments more than 6.5 mm. long, sepals more than 3.5 mm. long; leaves broadly lanceolate, the base cordate with descending lobes (rarely diverging or converging); relatively stout vines with few lateral branches. Plants of Texas and Mexico.
        e. Column relatively long; stigma-head apiculate; leaves about twice as long as broad; peduncle usually shorter than the subtending leaves or obsolete. Plants of central Mexico ..... 8. *S. elegans*
        ee. Column relatively short; stigma-head obscurely bilobed; leaves about three or more times as long as broad; peduncle usually exceeding the subtending leaves. Plants of Texas and northern Mexico ..... 9. *S. Torreyi*
      dd. Corolla lobes less than 6.5 mm. long, sepals less than 3 mm. long; leaves lanceolate to linear, the base cordate with diverging (rarely descending or converging) lobes, or obtuse to cuneate.
        e. Leaves broadly lanceolate to linear, the base cordate or hastate (rarely obtuse); ring of the corona free from the corona vesicles ..... 10. *S. cynanchoides*
        ee. Leaves narrowly lanceolate to linear or oblanceolate, the base obtuse to cuneate; ring of the corona adnate to the base of the corona vesicles.

f. Leaves narrowly lanceolate to linear; stems and leaves densely canescent; corolla lobes 4–5 mm. long. Plants of the southwestern United States..... 11. S. *hirtellum*

ff. Leaves oblanceolate; stems and leaves puberulent; corolla lobes 4.5–6.0 mm. long. Plants of Baja California..... 12. S. *arenarium*

4. SARCOSTEMMA BILOBUM Hook. & Arn. Bot. Beech. Voy. 438. 1841.

KEY TO THE SUBSPECIES

a. Leaves broadly ovate-cordate to orbicular, acuminate to submucronate; pollinium-sacs oblongoid-cylindrical, about four times as long as broad, the corpusculum narrowly sagittate; vesicles of the corona widest above the middle..... 4a. S. *bilobum* ssp. *bilobum*

aa. Leaves oblong-orbicular, mucronate; pollinium-sacs quadrate-oblongoid, somewhat flattened, two or three times as long as broad, the corpusculum broadly sagittate; vesicles of the corona widest below the middle..... 4b. S. *bilobum* ssp. *Lindenianum*

4a. SARCOSTEMMA BILOBUM Hook. & Arn. ssp. **bilobum** (Hook. & Arn.) R. Holm, stat. nov.

Sarcostemma bilobum Hook. & Arn. Bot. Beech. Voy. 438. 1841. (T.: *Beechey Herb. s. n. in Herb. Kew.*!).
Philibertia biloba (Hook. & Arn.) Gray, in Proc. Amer. Acad. 21:395. 1886.
Philibertia refracta Donn. Sm. in Bot. Gaz. 18:207. 1893. (T.: *Gomez 787 in U. S. Nat. Herb.*!).
Funastrum refractum (Donn. Sm.) Schltr. in Fedde's Repert. 13:287. 1915.
Funastrum bilobum (Hook. & Arn.) Macbr. in Contr. Gray Herb. n. s. 49:51. 1917.
Sarcostemma bellum Standl. & L. Wms. in Ceiba 1:90. 1950, ex char.

Stems twining or trailing, green, glabrescent to puberulous-pilose; lateral branches normally few. Leaves broadly ovate-cordate to orbicular, acuminate to submucronate, deeply cordate, the lobes usually converging, 3–5 cm. long, 2–5 cm. wide, membranaceous to subcoriaceous, glabrescent to puberulent on both surfaces, with one or more glands on the midrib at the base; petiole 1.5–3.0 cm. long. Inflorescences umbelliform, 9- to 44-flowered; peduncle 4–5 cm. long, glabrescent to puberulent; bracts usually linear, 1–2 mm. long, occasionally foliaceous and lanceolate; pedicels slender, 1.5–3.0 cm. long, more or less puberulent. Calyx lobes narrowly lanceolate, 2–3 mm. long, puberulent on both surfaces; squamellae absent or solitary. Corolla rotate-subcampanulate, yellowish-white, the tube 1.5 mm. long, the lobes reflexed at maturity, narrowly ovate, obtuse, revolute, 5–6 mm. long, glabrous to puberulous-papillate without, minutely pilosulose within, obscurely ciliolate. Gynostegium 3.0–3.5 mm. high, the column 1.5 mm. long. Anthers 1.5 mm. long, the apical appendage orbicular, emarginate, the pollinium-sacs oblongoid-cylindrical, 1 mm. long, with narrowly sagittate corpusculum; ring of the corona prominent, 1 mm. long, not adnate to the base of the corona vesicles; vesicles of the corona pyramidal, widest above the middle, 1.5–2.0 mm. long. Ovaries 1.5–2.0 mm. long, glabrous, the styles very sparsely pilosulose; stigma-head obscurely 2-apiculate. Follicles narrowly fusiform, attenuate, 8 cm. long, 1.5 cm. thick, minutely puberulent; seeds unequally biconvex, 5 mm. long, 3 mm. wide, rugose-papillate dorsally, papillate ventrally; coma about 3 cm. long.

The systematics of the Central America Sarcostemmas with reflexed corolla lobes long has been confused. A number of species have been described on the

basis of slight differences, chiefly in pubescence, and the names *S. odoratum* and *S. elegans* have been misapplied to these plants. Considering the problem as a whole I have been unable to distinguish more than one species, which is quite distinct from the true *S. odoratum*. At least two infraspecific entities are present, however, and their intergradation and enigmatic distribution still leave the taxonomy in an unsettled state. I have recognized two subspecies separated by the characters given in the key, together with other less tangible differences. *Sarcostemma b. bilobum* occurs, chiefly to the north and west, in Central America and southern Mexico. The putative hybrids have been designated as such since they do not appear to be part of a cline. Ecological data are sadly lacking; if available, they might explain the peculiar distribution of the subspecies. *Sarcostemma b. bilobum* apparently grows in open woods from 3000 to 9000 feet, and flowers from October to December.

MEXICO. CHIAPAS: between Teneapa and Yajalon, *E. W. Nelson 3265;* near Yajalon, *E. W. Nelson 3412.* COLIMA: Paso del Río, *Emrick 178.* JALISCO: Santa Cruz de Vallarta, *Mexia 1271.* MEXICO: Temascáltepec, *Hinton 8473.* MICHOACÁN: Coalcomán, Coahuayana, *Hinton 16249.* MORELOS: near Cuernavaca, *Pringle 11887.* OAXACA: Capital Concordia, *Reko 3513;* near Tehuantepec?, *Seler & Seler 1790.* YUCATÁN: Izamál, *Gaumer 880* (in part).

GUATEMALA. PETÉN: Uaxactun, *Bartlett 12470.* SACATEPEQUEZ: Santiago, *Gomez 787,* type of *P. refracta* Donn. Sm.

HONDURAS. MORAZAN: Río El Quebracho above Jicarito, *Standley 14814,* type of *S. bellum* Standl. & L. Wms.

BRITISH HONDURAS: Honey Camp, *Lundell LP33, 609.*

PUTATIVE HYBRIDS: listed following *S. bilobum Lindenianum* (4b).

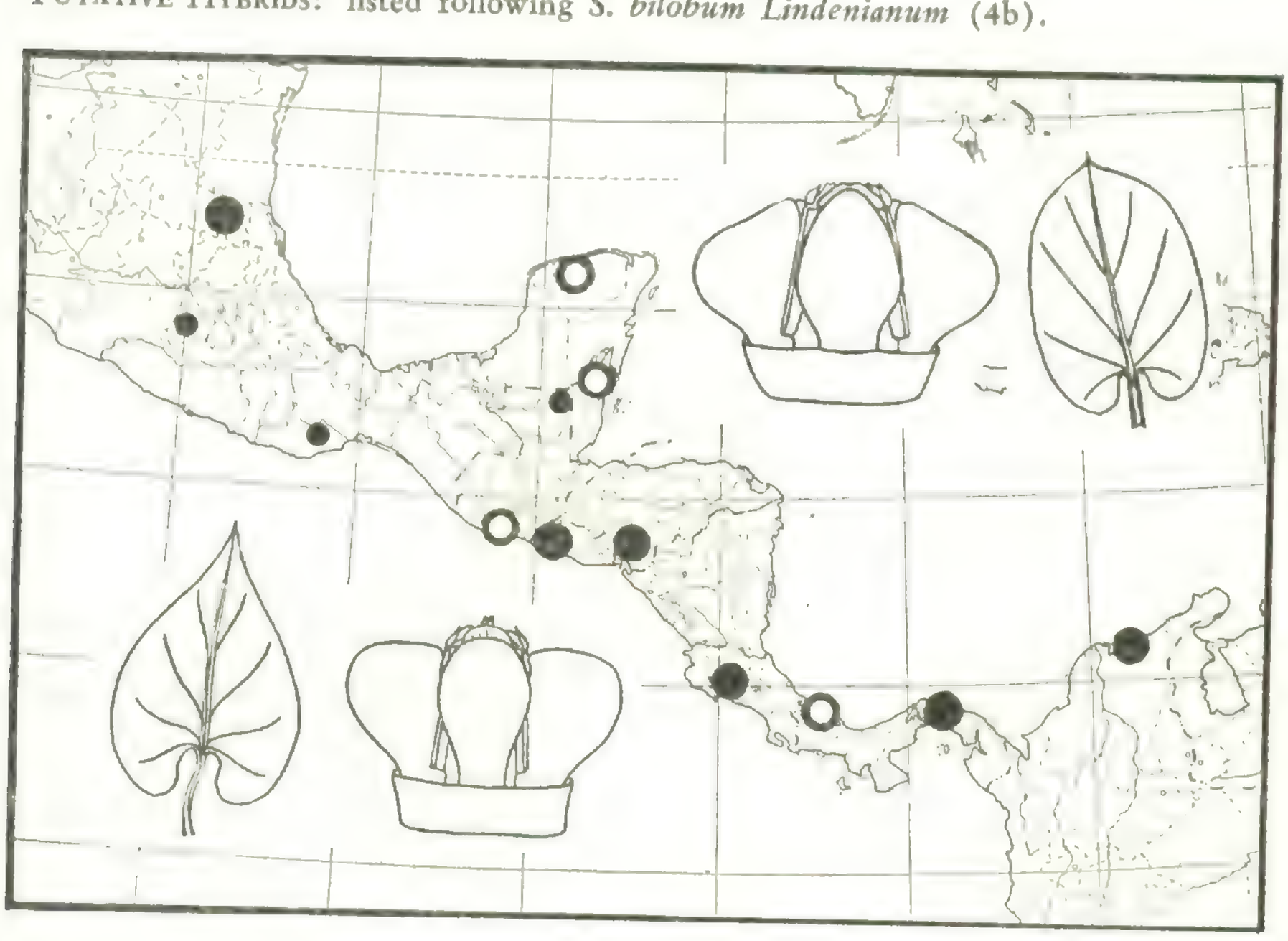

Fig. 8. Gynostegium and leaf of *S. bilobum bilobum* (lower left), of *S. bilobum Lindenianum* (upper right); distribution of *S. bilobum bilobum* (small dots), of *S. bilobum Lindenianum* (large dots), of putative hybrids, black circles.

4b. SARCOSTEMMA BILOBUM Hook. & Arn. ssp. **Lindenianum** (Decne.) R. Holm, stat. nov.

Sarcostemma Lindenianum Decne. in DC. Prodr. 8:541. 1844. (T.: *Linden s. n. in Herb. Paris*!).
Philibertia Lindeniana (Decne.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:318. 1881.
Philibertia Ervendbergii A. Gray, in Proc. Amer. Acad. 21:395. 1886. (T.: *Ervendberg 174 in Herb. Gray*!).
Philibertia Fendleri A. Gray, loc. cit. 1886. (T.: *Fendler 2119 in Herb. Gray*!).
Philibertia reflexa Pittier, in Contr. U. S. Nat. Herb. 13:96. 1910. (T.: *Pittier s. n. in U. S. Nat. Herb.*!).
Philibertia dumetorum T. S. Brandeg. in Univ. Calif. Publ. Bot. 4:380. 1913. (T.: *Purpus 6013 in Herb. Univ. Calif.*!).
Funastrum Ervendbergii (Gray) Schltr. in Fedde's Repert. 13:285. 1915.
Funastrum Fendleri (Gray) Schltr. loc. cit. 1915.
Funastrum Lindenianum (Decne.) Schltr. loc. cit. 286. 1915.
Funastrum reflexum (Pittier) Schltr. loc. cit. 287. 1915.
Philibertella filipes Rusby, Descr. S. Am. Pl. 94. 1920. (T.: *H. H. Smith 1669 in Herb. N. Y. Bot. Gard.*!).
Funastrum dumetorum (Brandeg.) Standl. in Contr. U. S. Nat. Herb. 23:1172. 1924.

Stems trailing or twining, gray-green, pilosulose; lateral branches normally few. Leaves oblong-orbicular, mucronate, deeply cordate, the lobes usually converging, 2–5 cm. long, 1.5–4.0 cm. wide, subcoriaceous, densely pilosulose on both surfaces, rarely glabrous, with one or more glands on the midrib at the base; petiole 1.0–2.5 cm. long. Inflorescences umbelliform, 7- to 10-flowered; peduncle 1.5–2.0 cm. long, subpilose; bracts usually linear, minute, occasionally foliaceous and ovate; pedicels 1–2 cm. long, subpilosulose. Calyx lobes linear to ovate, 2.5 mm. long, pilosulose without, glabrate within; squamellae usually solitary. Corolla rotate-subcampanulate, whitish with a median purple streak on each lobe, the tube 2 mm. long, the lobes reflexed at maturity, lanceolate, obtuse, 5.5 mm. long, glabrescent without, appressed-pilosulose within, ciliolate. Gynostegium 4 mm. high the column 1.5 mm. long. Anthers 1.5 mm. long, the apical appendage reniform, emarginate, the pollinium-sacs quadrate-oblongoid, somewhat flattened, 0.8 mm. long, with broadly sagittate corpusculum; ring of the corona thick, revolute, not adnate to the base of the corona vesicles; vesicles of the corona pyramidal, widest below the middle, 2 mm. long. Ovaries 2 mm. long, glabrous; stigma-head abruptly 2-apiculate to umbonate. Follicles obclavate, attenuate, 7 cm. long, 2 cm. thick, puberulent, finely striate; seeds somewhat flattened, 7 mm. long, 4 mm. wide, minutely papillate on both surfaces; coma about 3 cm. long.

The relationship of this subspecies with S. *b. bilobum* has been described in the discussion of the latter. *Sarcostemma b. Lindenianum* occurs, roughly to the south and east, in Mexico and Central America and extends into Colombia and Venezuela. The few data available indicate that it is found at much lower altitudes, from 50 to 80 feet above sea level, and blooms from July to September. Thus the isolating mechanisms may be in part ecological. I believe that mechanical difficulties attendant with hybridization also play an important part, in view of the differences in the pollinia.

MEXICO. CHIAPAS: Tonalá, *Purpus 6651*. SAN LUIS POTOSÍ: Rascón, *Purpus 5494, 5256*. VERA CRUZ: Acasonica, *Purpus 8412*; Baños del Corizál, *Purpus 6013*, type of *P. dumetorum* Brandeg.; Wartenburg, near Tantoyuca, *Ervendberg 174*, type of *P. Ervendbergii* Gray. YUCATÁN: Izamál, *Gaumer 880* (in part).

HONDURAS. VALLE: San Lorenzo, *Rodriguez 3486, 3331*.

EL SALVADOR: Acajutla, *Calderón 1676*.

COSTA RICA: near San Mateo, *Biolley 7095*; Nicoya, *Pittier s. n.*, type of *P. reflexa* Pittier; vic. Cascajál, 25 km. ESE of Puntarenas, *Holm & Iltis 272*.

PANAMA. PANAMA: banks of Mamoni River, above Chepo, *Pittier 4728*.

COLOMBIA. MAGDALENA: Santa Marta, *H. H. Smith 1669*, type of *P. filipes* Rusby.

VENEZUELA. MÉRIDA: Tovar, *Fendler 2119*, type of *P. Fendleri* Gray.

PUTATIVE HYBRIDS. MEXICO. YUCATÁN: Izamál, *Gaumer 880* (in part). PANAMA. BOCAS DEL TORO: near Chiriquí Lagoon, *Wedel 1755*. GUATEMALA. ESCUINTLA: Santa Lucía, *Heyde & Lux 47, 6353*. BRITISH HONDURAS: Corozál District, Santa Rita, *Gentle 829*; San Andrés, *Gentle 553*.

5. SARCOSTEMMA **odoratum** (Hemsl.) R. Holm, comb. nov.

Philibertia odorata Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:319. 1881. (T.: *Salvin s. n. in Herb. Kew.*!).
Funastrum odoratum (Hemsl.) Schltr. in Fedde's Repert. 13:286. 1915.

Stems twining, gray-green, pilosulose to pilose; lateral branches normally few. Leaves narrowly to broadly ovate, long-mucronate, deeply cordate, the lobes converging, 3.5–5.0 cm. long, 2.0–4.5 cm. wide, subcoriaceous, pilosulose above, densely puberulous-pilose beneath, with one or more glands on the midrib at the base; petiole 2.5–4.0 cm. long. Inflorescences umbelliform, 6- to 12-flowered; peduncle 1.5–3.0 cm. long, pilosulose; bracts linear, minute; pedicels 1.5–2.0 cm. long, pilosulose. Calyx lobes narrowly lanceolate, 4 mm. long, subpilose without, glabrous within; squamellae usually solitary. Corolla rotate-subcampanulate, white, the tube 1 mm. long, the lobes ovate, 5 mm. long, pilosulose without, puberulous-papillate within. Gynostegium 2.5 mm. high, the column nearly obsolete. Anthers 1.5 mm. long, the apical appendage deltoid, the pollinium-sacs cylindrical, 0.75 mm. long, with sagittate corpusculum; ring of the corona thick, revolute, scarcely adnate to the base of the corona segments; vesicles of the corona ovoid, 2 mm. long. Ovaries 1.5 mm. long, glabrous; stigma-head abruptly 2-apiculate. Follicles and seeds unknown.

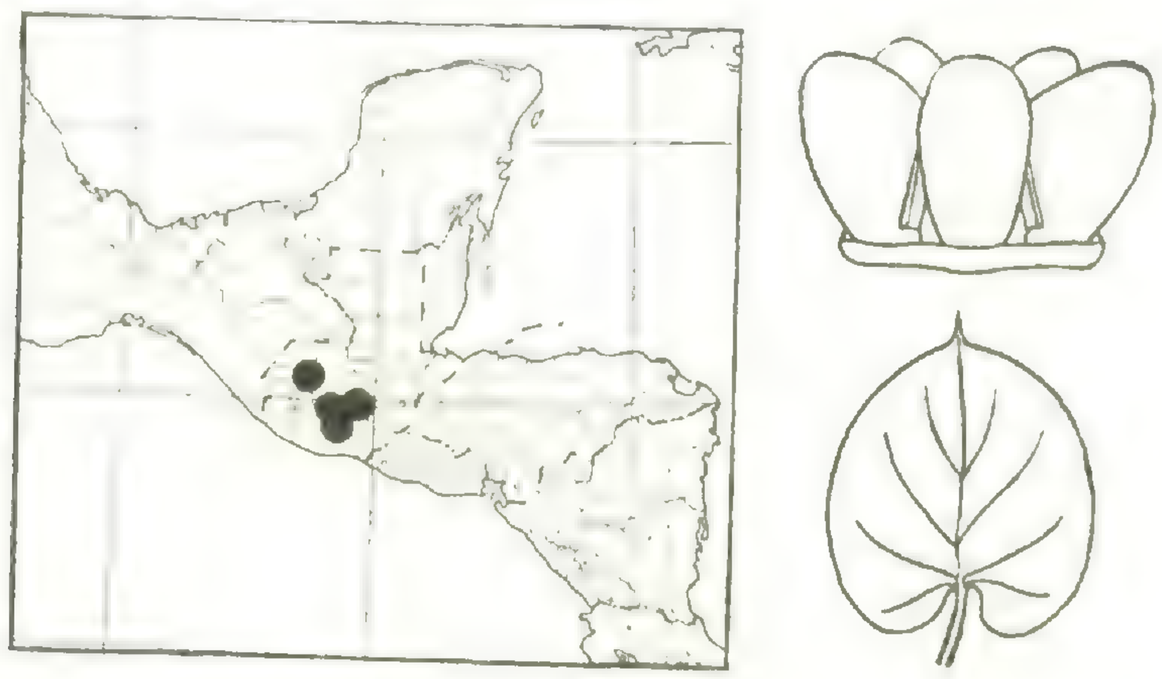

Fig. 9. Distribution, gynostegium and leaf of *S. odoratum*.

Sarcostemma odoratum is a rare species known only from Guatemala. The converging basal lobes of the leaves and characters of the gynostegium ally it with S. *bilobum;* it lacks the long column and reflexed corolla lobes of that species, however. It has been collected on hillsides from 4000 to 5000 feet; apparently it flowers from August to September.

GUATEMALA. CHIMALTENANGO: Chimaltenango, *J. R. Johnston 752*. GUATEMALA: *Aguilar 313*. HUEHUETENANGO: between San Sebastian H. and large peñasco above town, *Steyermark 50514*. SACATEPEQUEZ: Volcán de Fuego, *Salvin s. n.*, type of *P. odorata* Hemsl. DATA INCOMPLETE: Brenas, *Tonduz 785*.

6. SARCOSTEMMA GRACILE Decne. in DC. Prodr. 8:539. 1844. (T.: *Tweedie 1837 in Herb. Kew.*!).

Amphistelma exsertum Griseb. Symb. Fl. Arg. 229. 1879, ex char. (T.: *Lorentz & Hieronymous 1125*).
Sarcostemma carpophylloides Morong, Enum. Pl. Paraguay (Ann. N. Y. Acad. Sci. 7:) 165. 1893. (T.: *Morong 1004 in Herb. N. Y. Bot. Gard.*!).
Philibertia exserta (Griseb.) Schltr. in O. Ktze. Rev. Gen. 3:200. 1898.
Ceramanthus gracilis (Decne.) Malme, in Ark. Bot. 4^{14}:2. 1905.
Funastrum gracile (Decne.) Schltr. in Fedde's Repert. 13:285. 1915.

Stems twining, green, glabrous, the nodes puberulent; lateral branches many. Leaves narrowly lanceolate or linear, acute to acuminate, obtuse to cuneate, involute proximally 1–2 mm., 3.0–5.5 mm. long, 0.2–0.5 cm. wide, membranaceous, glabrate to minutely puberulent above and beneath, with no glands on the midrib at the base; petiole 0.1 cm. long. Inflorescences umbelliform, 8- to 16-flowered; peduncle 3.5–7.0 cm. long, glabrate to very minutely puberulent; bracts linear, minute; pedicels 0.9–1.5 cm. long, pilosulose. Calyx lobes lanceolate, 1.5 mm. long, minutely pubescent without, glabrous within; squamellae absent. Corolla rotate-subcampanulate, white, the tube 1 mm. long, the lobes reflexed, ovate, acute, 3.5 mm. long, glabrate without, minutely papillate within ciliolate. Gynostegium 2 mm. high, the column 1.5 mm. long. Anthers 1 mm. long, the apical appendage reniform, the pollinium-sacs oblongoid-cylindrical, 0.75 mm. long with sagittate corpusculum; ring of the corona thick, adnate to the base of the corona vesicles, vesicles of the corona ovoid, pointed at the tip, 1.5 mm. long. Ovaries 1.5 mm. long, essentially glabrous; stigma-head conical, obscurely 2-lobed. Follicles narrowly fusiform, 3.5–5.5 cm. long, 0.4–0.5 cm. thick, minutely puberulent; seeds somewhat flattened, 4 mm. long, 1.5 mm. wide, the margin flat and obscurely serrate; coma about 1 cm. long.

The small flowers with reflexed corolla lobes and the linear leaves separate this species at once from all other South American forms. Since it is distant from any species remotely resembling it, I hesitate to speculate as to its affinities. There is something reminiscent of S. *glaucum* in the floral structure and inflorescence, but the species hardly can be referred to series CLAUSA since the peduncle does not équal the stem in thickness and only rarely bears two cymes. This species may represent an extreme modification of the ancestral form of series CLAUSA.

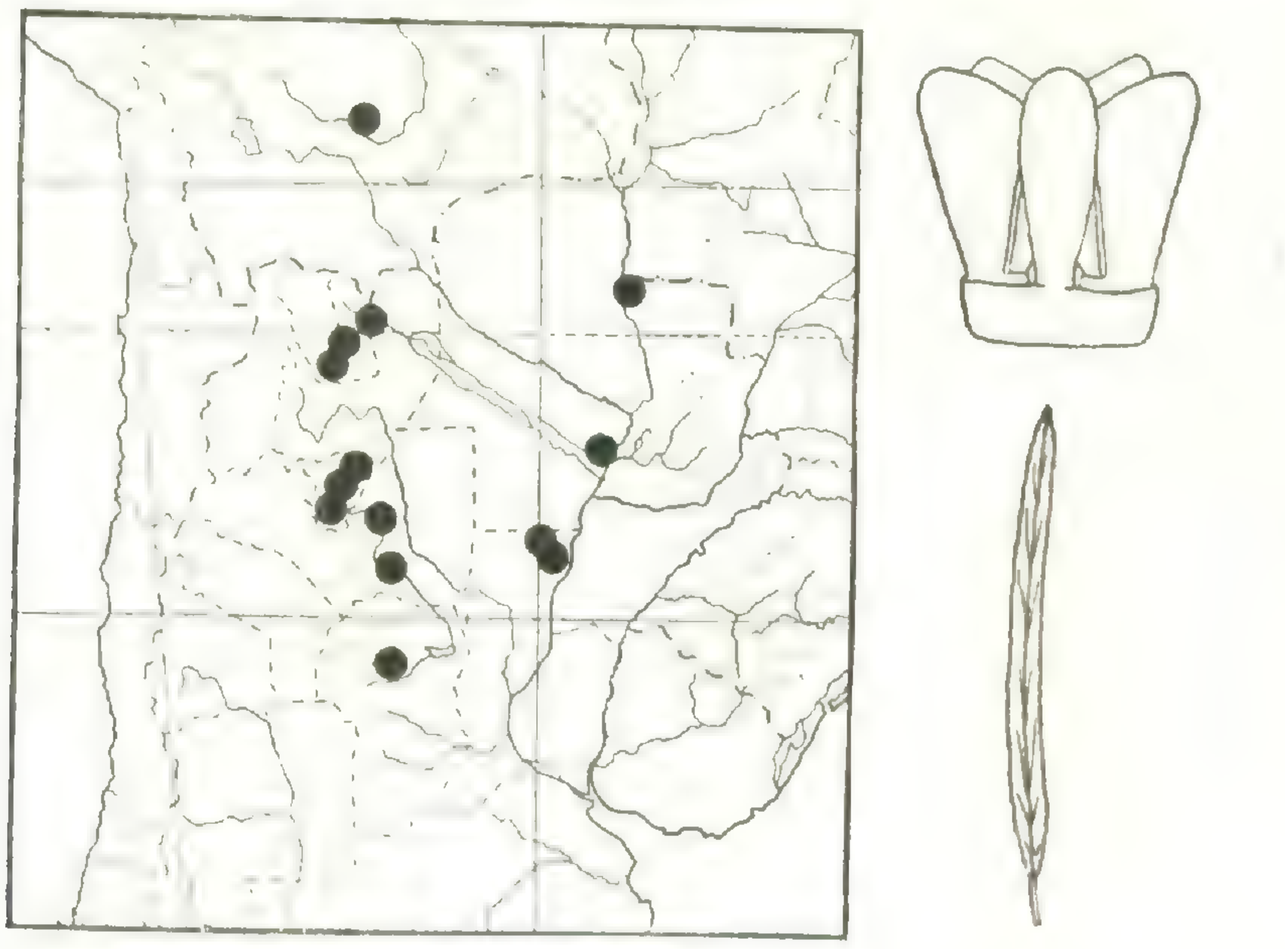

Fig. 10. Distribution, gynostegium, and leaf of *S. gracile*.

Sarcostemma gracile inhabits the *llanos* of northern Argentina and adjacent Bolivia and Paraguay. According to Meyer, it is halophytic, a fact which may account for its obvious reduction. It flowers from October to March.

BOLIVIA. SANTA CRUZ: Chilón, *Steinbach 3964*. CHACO: Curupenda, *Cárdenas 2521*; Tatarenda, *Fries 1441*.

PARAGUAY: Chaco Paraguayo, Puerto Casado, *Rojas 2482*; Santa Elisa, *Rojas 2715*; Pilcomayo River, *Morong 1004*, type of *S. carpophylloides* Morong.

ARGENTINA. CATAMARCA: Capitál, *Castillón 1065*. CHACO: Fontana, *T. Meyer 219*. CÓRDOBA: Córdoba, *Kurtz 4510, Lassen 86*; Sierra Chica, *Kurtz 207*. FORMOSA: Formosa, *Jörgensen 2599*; Las Lomitas, *Parodi 8436*. JUJUY: San Pedro, *Venturi 5318*; Perico del Carmen, Estancia Peruco, *Venturi s. n.* LA RIOJA: Famatina, *Venturi 7828*; La Antigua, Pozo de la Orilla, *Castellanos s. n.* SALTA: Orán, Tartagal Villa, *Schreiter 10844, 3573*; 5 km. NW Embarcación, *West 8443*. SANTA FE: Generál Obligado, Los Amores, *Ragonese 3115*. SANTIAGO DEL ESTERO: La Banda, *Lillo 6091*; Recreo, *Stuckert 23009*; between Brea Pozo & Río Huayco Hondo, *Bartlett 19753*. TUCUMÁN: Burruyacu, El Timbo, *Venturi 1718*; Río Lules, *Lillo 7860*; Cruz Alta, Orillas Río Sali, *Venturi 753*; Campo Alegre, *Schreiter 5915*; Famailla, Bella Vista, *Venturi 2730*.

7. SARCOSTEMMA CRISPUM Benth. Pl. Hartw. 291. 1848. (T.: *Hartweg s. n.*!).

Sarcostemma heterophyllum Engelm. ex Torr. Pac. R. R. Rept. 5(App.):362. 1857. (T.: *Wright 1679*!).

Sarcostemma undulatum Torr. in Bot. Mex. Bound. Surv. 161. 1859. (T.: *Parry s. n.*!).

Philibertia undulata (Torr.) Gray, in Proc. Amer. Acad. 12:65. 1877.

Philibertia linearis (Decne.) A. Gray, var. *heterophylla* (Engelm. ex Torr.) Gray, Syn. Fl. 2^1:88. 1878, as to basinym only.

Philibertia crispa (Benth.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:318. 1881.

Philibertella crispa (Benth.) Vail, in Bull. Torr. Bot. Club 24:307. 1897.

Philibertella Hartwegii heterophylla (Engelm. ex Torr.) Vail, loc. cit. 1897, as to basinym only.

Philibertella heterophylla (Engelm. ex Torr.) Cocker. in Bot. Gaz. 26:279. 1898, as to basinym only.

Funastrum crispum (Benth.) Schltr. in Fedde's Repert. 13:284. 1915.

Funastrum lineare (Decne.) Macbr. var. *heterophyllum* (Engelm. ex Torr.) Macbr. in Contr. Gray Herb. n. s. 49:50. 1917, as to basinym only.
Funastrum heterophyllum (Engelm. ex Torr.) Standl. in Contr. U. S. Nat. Herb. 23:1170. 1924, as to basinym only.
Philibertia heterophylla (Engelm. ex Torr.) Jepson, Man. Fl. Pl. Calif. 770. 1925, as to basinym only.
Sarcostemma lobata Waterfall, in Rhodora 51:58. 1949. (T.: *Waterfall 7914 in Herb. Univ. Okla.*!).

Stems twining or trailing, green, glabrate to puberulent, the nodes densely white-pubescent; lateral branches few. Leaves narrowly to broadly lanceolate, acuminate, hastate, cordate or truncate, usually strikingly undulate-crispate, rarely not crispate, 3–10 cm. long, 0.5–3.0 cm. wide, subcoriaceous, puberulent above, the midrib usually white-pilose, without glands at the base, puberulent beneath, the midrib usually white-glabrous; petiole 0.4–0.8 cm. long. Inflorescences umbelliform, 4- to 7-flowered; peduncle 0.3–3.0 cm. long, glabrescent, much shorter than the subtending leaves; bracts linear, minute; pedicels 1.5–2.0 cm. long, glabrescent. Calyx lobes narrowly lanceolate, 3–6 mm. long, copiously puberulent on both surfaces; squamellae solitary, rarely paired. Corolla rotate-subcampanulate, greenish purple without, purple within, the tube 1 mm. long, the lobes ovate-elliptic, obtuse, 7–11 mm. long, puberulent without, glabrous within, ciliate. Gynostegium 3 mm. high, the column 1 mm. long. Anthers 1 mm. long, the apical appendage ovate, the pollinium-sacs oblongoid-cylindrical, 0.8 mm. long, with sagittate corpusculum; ring of the corona thin, revolute, scarcely adnate to the column; vesicles of the corona thin, revolute, scarcely adnate to the column; vesicles of the corona oblongoid-ovoid, constricted at their insertion upon the column, 1 mm. long. Ovaries 2 mm. long, glabrescent; stigma-head abruptly and shortly 2-apiculate. Follicles narrowly fusiform, long-attenuate, 8.5–12.3 cm. long, 1.3–1.9 cm. thick, puberulent, finely striate; seeds unequally biconvex, 7 mm. long, 3 mm. wide, obscurely rugose dorsally, minutely papillate ventrally; coma about 3 cm. long.

The crispate leaves and large, deep purple flowers combine to make this one of the most distinctive species in the genus. There is a poorly defined cline in the characters of the leaves: to the south and west the leaves generally are smaller, less crisped, and less pubescent on the midrib. I have seen specimens from Mexico which show no signs of crisping and have very narrowly lanceolate leaves. The ends of the cline are not sufficiently distinct for taxonomic recognition, however. I cannot conceive that this cline is the result of anything but a response to increasing aridity which leads to reduction of the lamina and consequent suppresion of the marginal growth responsible for crispature. Since floral differences do not exist, hybridization probably does not play a role.

The rather confused synonymy of this species is explained in the discussion pertaining to *Sarcostemma cynanchoides* ssp. *Hartwegii*. *Sarcostemma crispum* seems nowhere to be common; Reverchon reports it to be local and rare around Dallas, Midland, and Austin, Texas, and other collectors indicate that it usually

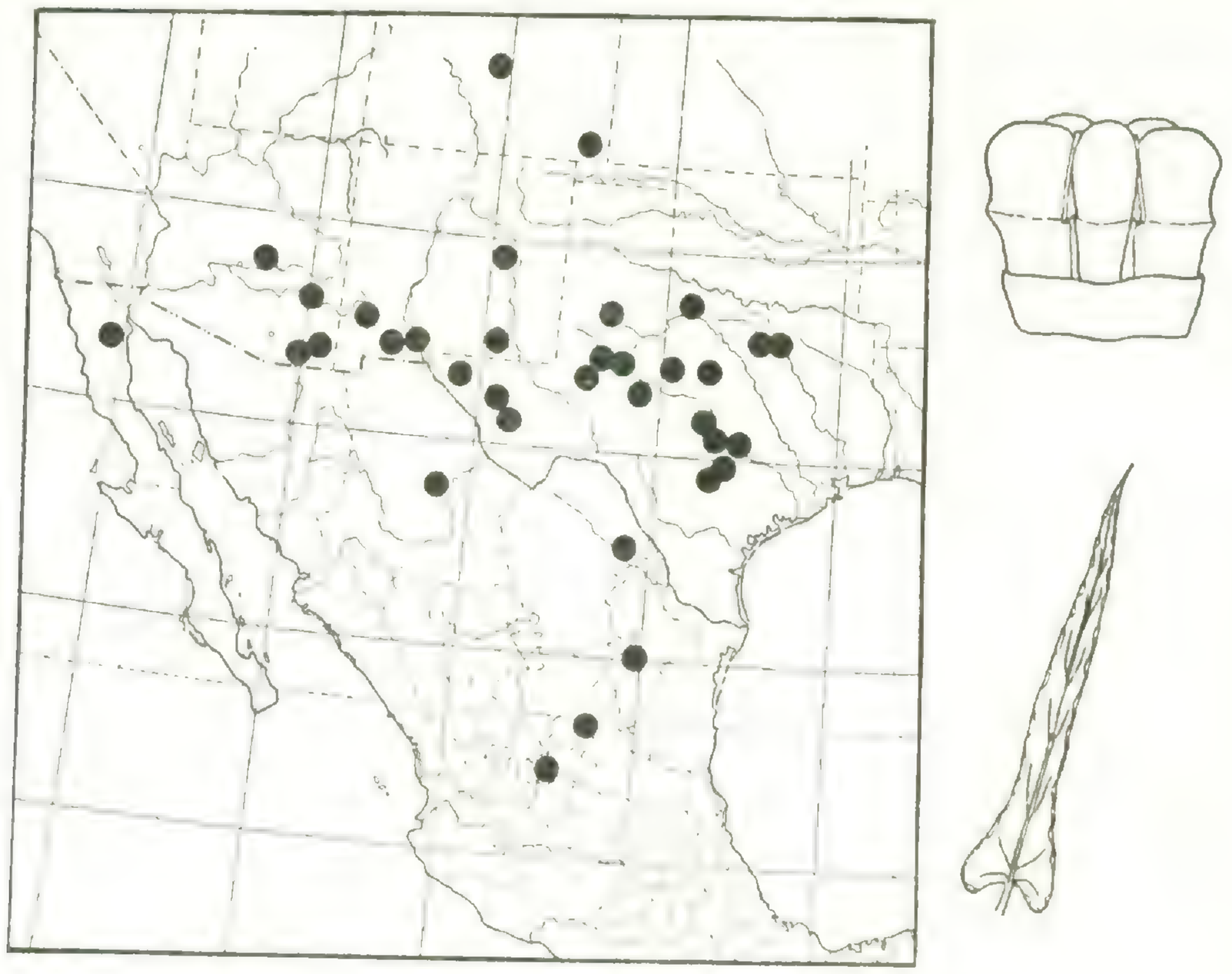

Fig. 11. Distribution, gynostegium, and leaf of S. *crispum*.

occurs scatteringly or in very small colonies. It grows at altitudes of 4000 to 7000 feet, chiefly in open, dry, rocky, or stony ground, and has been found in chaparral associated with *Zizyphus* and *Fallugia*. The blooming season ranges from May 9 to August 24. Fruiting specimens have been collected from May 13 to August 24. The distribution is from Colorado through Texas, New Mexico, and Arizona to central Mexico.

UNITED STATES. COLORADO: BACA CO.: S of Pritchett, *Harrington 3353*; FREMONT CO.: Phantom Canyon, *Christ 1090*. OKLAHOMA: CIMARRON CO.: N of Black Mesa, 3 mi. N of Kenton, *Waterfall 7914*, type of S. *lobata* Waterfall. TEXAS: BAYLOR CO.: Seymour, *Reverchon s. n.*; BEXAR CO.: San Antonio, *Schulz 793*; BLANCO CO.: *Wright 1678*; BREWSTER CO.: *Ferris & Duncan 2631*; CALLAHAN CO.: Baird, *E. J. Palmer 13688*; COMAL CO.: Fischer's Store, *E. J. Palmer 12200*; DALLAS CO.: Dallas, *Reverchon 601*; EASTLAND CO.: Eastland, *Oyster 2595*; GILLESPIE CO.: Grape Creek, *Jermy 134*; HOWARD CO.: Big Spring, *Eggert s. n.*; HUDSPETH CO.: Eagle Mts. near Hot Wells, *Waterfall 4964*; JEFF DAVIS CO.: Limpia, *Young 27*; LLANO CO.: *Bray 336½*; LUBBOCK CO.: Lubbock, *Reed 3694*; MIDLAND CO.: Midland, *Tracy 7080*; MITCHELL CO.: Colorado, *Eggert s. n.*; TARRANT CO.: *Ruth 740*; TAYLOR CO.: Abilene, *Tracy 7979*; TOM GREEN CO.: Dove Creek, *Tweedy 235*; TRAVIS CO.: Austin, *E. Hall 518*. NEW MEXICO: DONA ANA CO.: Organ Mts., *Wooton s. n.*; EDDY CO.: Queen, *Wooton s. n.*; GRANT CO.: Central, *Mulford 406*; GUADALUPE CO.: Santa Rosa, *Arsène 19470*; LUNA CO.: Deming, *Goldman 1445*. ARIZONA: COCHISE CO.: Rhoda Rigg's Ranch, Chiricahua Mts., *Blumer 1400*; GILA CO.: Collom Camp, Matzatzal Mts., *Collom 575*; GRAHAM CO.: 10 mi. above Clifton, *Hough s. n.*

MEXICO. BAJA CALIFORNIA NORTE: near Ciénaga, S end of Sierra Juárez, *Wiggins 9148*. CHIHUAHUA: near Chihuahua, *Pringle s. n., 546, 1326*; W from Pearson, *Barlow s. n.*; Sta. Eulalia Plains, *Wilkinson s. n.* COAHUILA: 5 km. NE Sta. Elena, *R. M. Stewart 605*; 2–3 km. N Puerto Colorado, *I. M. Johnston 8681*; San Lázaro, *Wynd & Muller 101*. NUEVO LEON: 15 miles SW Galeana, *Muller & Muller 1084*. SAN LUIS POTOSÍ: Charcas, *Lundell 5074*.

8. SARCOSTEMMA ELEGANS Decne. in DC. Prodr. 8:541. 1844. (T.: *Berlandier 602 in Herb. Paris*!).

Sarcostemma bicolor Decne. loc. cit. 1844. (T.: *Galeotti 1537 in Herb. Paris*!).
Sarcostemma luridum Kunze, in Linnaea 20:26. 1847, ex char. (T.: *Schleiden s. n.*).
Philibertia elegans (Decne.) Hemsl. in Godm. & Salv. Biol. Centr.-Amer. Bot. 2:318. 1881.
Philibertia lurida (Kze.) Hemsl. loc. cit. 319. 1881.
Philibertia bicolor (Decne.) Gray, in Proc. Amer. Acad. 21:395. 1886.
Philibertella elegans (Decne.) Vail, in Bull. Torr. Bot. Club 24:310. 1897.
Funastrum elegans (Decne.) Schltr. in Fedde's Repert. 13:284. 1915.
Funastrum luridum (Kze.) Schltr. loc. cit. 286. 1915.
Funastrum bicolor (Decne.) Macbr. in Contr. Gray Herb. n. s. 49:50. 1917.
Funastrum bicolor (Decne.) Standl. in Contr. U. S. Nat. Herb. 23:1172. 1924.

Stems twining or trailing, gray-green, glabrescent to copiously pilosulose; lateral branches few. Leaves broadly lanceolate to oblong, acute to mucronate, deeply cordate, the lobes descending, 2–5 cm. long, 1.0–4.5 cm. wide, subcoriaceous, glabrescent to copiously puberulent on both surfaces, with one or more glands on the midrib at the base; petiole 0.6–2.2 cm. long. Inflorescences umbelliform, 4- to 7-flowered; peduncle 0.5–1.8 cm. long, minutely puberulent, much shorter than the subtending leaves; bracts linear, 0.1–0.2 cm. long; pedicels 1.0–2.5 cm. long, puberulent. Calyx lobes ovate, 4–6 mm. long, densely puberulent without, puberulent within; squamellae alternate, usually solitary. Corolla rotate-subcampanulate, yellow, with a deep purple spot at the base of each lobe, often extending upward as a median streak, or entirely suffused with purple on the inner surface, greenish without, the tube 3.5 mm. long, the lobes ovate-lanceolate, obtuse, 9–13 mm. long, minutely puberulent without, glabrescent within. Gynostegium 3.5 mm. high, the column about 1 mm. long. Anthers 1.5 mm. long, the apical appendage suborbicular, the pollinium-sacs oblongoid-cylindrical, 0.7 mm. long, with sagittate corpusculum; ring of the corona thin, adnate to the base of the corona vesicles; vesicles of the corona oblongoid to subspheroid, the inner side often apiculate at the tip, or with a vertical keel, 2.5 mm. long. Ovaries 2.5 mm. long, glabrous; stigma-head conical, with 2 long apiculae. Follicles narrowly fusiform-obclavate, 7.6 cm. long, 1.2 cm. thick, minutely puberulent, finely striate; seeds unequally biconvex, 7 mm. long, 3 mm. wide, obscurely rugose on both surfaces; coma about 3 cm. long.

Sarcostemma elegans is closest, morphologically, to S. *Torreyi,* from which it differs in the short peduncles, relatively short leaves, and the long, apiculate stigma-head. S. *elegans* occurs in the Central Plateau region of Mexico, while S. *Torreyi* is found in the northern desert areas of Mexico and adjacent Texas. As indicated in the key, the two species form a close-knit group more or less isolated from the other species in the section. Probably they have either differentiated from a common ancestor occupying the area from central Mexico to Texas, or the southern species may have migrated to the north giving rise to S. *Torreyi* in this changed habitat. The floral differences between the species are such that hybridization would appear to be difficult, e. g. the length of the column and stigma-head

appendages in S. *elegans* would result in the pollinia being affixed to different insects or to different places upon the same species of insect. There is a narrow gap in the ranges; however, there are several specimens *(Stanford, Retherford & Northcraft 869, Reko 5259)* which I interpret as hybrids between S. *elegans* and S. *Torreyi*. Apparently these are back-crosses, for they are sufficiently close to one or the other of the putative parents to be easily referred to either species. The precise effects of this hybridization cannot be determined without the use of population studies. The most satisfactory way of handling such a problem taxonomically appears to be to refer the hybrids to whichever species they are morphologically and geographically closest. Unfortunately, this has the disadvantage of obscuring the interesting genetic implications. *Funastrum vesiculare* apparently is a hybrid which is very close to S. *Torreyi*, from which it differs, however, in the direction of S. *elegans;* I have referred it to the former species.

Sarcostemma elegans has been found growing chiefly on rocky slopes or lava fields at altitudes from 5000 to 8000 feet. Flowering specimens are dated from January 1 to October 27; the single fruiting specimen is dated August 2.

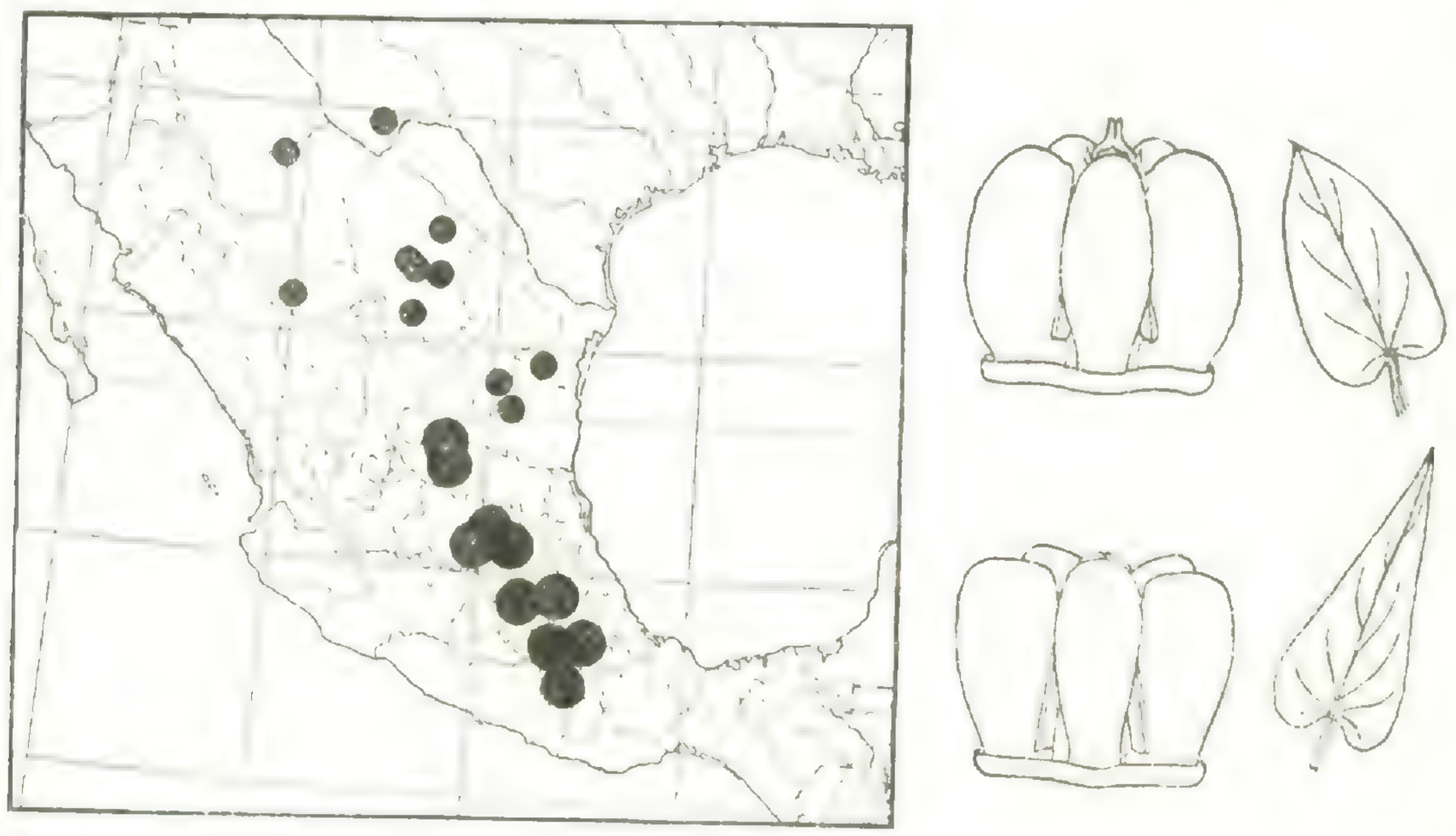

Fig. 12. Gynostegium and leaf of S. *elegans* (upper row), of S. *Torreyi* (lower row). Distribution of S. *elegans* (large dots), of S. *Torreyi* (small dots).

MEXICO. DISTRITO FEDERÁL: Pedregál, *Lyonnet 29;* San Gerónimo, *Russell & Souviron 127;* near Mexico City, *Berlandier 602*, type of S. *elegans* Decne. GUANAJUATO: Guanajuato, *Duges 101.* HIDALGO: Ixmilquilpan, *Purpus 1379; Rose, Painter & Rose 8943.* JALISCO: near Zapotlán, *Pringle 5496.* MÉXICO: Temascáltepec, Socobon, *Hinton 7225;* Crucero Agua Blanca, *Hinton 4936;* Valley of México, near San Angel, *Rose, Painter & Rose 9400;* near Tlalpam, *Rose, Painter & Rose 8250, Pringle 13116, Rose & Hough 4529;* Santa Fe, *Bourgeau 318.* MICHOACÁN: Coalcomán, Barroloso, *Hinton 15075.* OAXACA: Nochixtlan, barrancas de Puebla Viejo, *Conzatti 1842;* Tenango, *L. C. Smith 390.* PUEBLA: near San Luis Tultitlanapa, *Purpus 3241;* near Tehuacán, *Pringle 6760, Mohr s. n., Rose, Painter & Rose 9053, Galeotti 1537*, type of S. *bicolor* Decne.; El Riego, *Purpus 1258;* Rancho Posado, *Nicolas 47.* QUERETARO: near San Juan del Río, *Rose, Painter & Rose*

9669, Altamirano 1973. SAN LUIS POTOSÍ: Bocas, *Pringle 3564;* Silos, *Purpus 482;* near San Luis Potosí, *Parry & Palmer 589, Schaffner 316;* mts. near San Miquelito, *Schaffner 649.* TLAXCALA: Tlaxcala, *Balls 4908.* VERA CRUZ: Orizaba, *Botteri 979.*

9. SARCOSTEMMA TORREYI (Gray) Woods. in Ann. Mo. Bot. Gard. 28:217. 1941.

Philibertia Torreyi A. Gray, in Proc. Amer. Acad. 12:64. 1877. (T.: *Parry s. n.*!).
Philibertella Torreyi (Gray) Vail, in Bull. Torr. Bot. Club 24:309. 1897.
Funastrum Torreyi (Gray) Schltr. in Fedde's Repert. 13:287. 1915.
Funastrum vesiculare Woods. in Amer. Jour. Bot. 22:687. 1935. (T.: *Bartlett 10318 in Herb. Univ. Mich.*!).

Stems twining or trailing, gray or green, pilosulose; lateral branches few. Leaves lanceolate, acuminate to acute, cordate, the lobes descending, 1.5–4.0 cm. long, 1.0–2.5 cm. wide, subcoriaceous, pilosulose on both surfaces with one or more glands on the midrib at the base; petiole 0.7–1.4 cm. long. Inflorescences umbelliform, 7- to 10-flowered; peduncle 1.0–3.5 cm. long, pilosulose; bracts linear, 0.1–0.2 cm. long; pedicels 0.8–1.6 cm. long, pilosulose. Calyx lobes ovate-lanceolate, 4–6 mm. long, puberulent on both surfaces; squamellae solitary, rarely paired. Corolla rotate-subcampanulate, cream-colored with a purple spot at the base and a median purple spot on each lobe, lobes ovate, acute, 7–11 mm. long, minutely puberulent without, glabrate within, scarious-ciliate. Gynostegium 3 mm. high, the column very short. Anthers 1.5 mm. long, the apical appendage suborbicular to subreniform, the pollinium-sacs oblongoid-cylindrical, 0.8 mm. long, with sagittate corpusculum; ring of the corona fleshy, adnate to the base of the corona vesicles; vesicles of the corona oblongoid to obovoid, 2.5 mm. long. Ovaries 2.5 mm. long, glabrous; stigma-head subconical, obscurely bilobed. Follicles fusiform, long-attenuate, 8.2 cm. long, 1.2 cm. thick, finely striate; seeds somewhat flattened, 7 mm. long, 4 mm. wide, minutely papillate on both surfaces; coma about 3 cm. long.

A relatively rare and local species, the relations of which to *S. elegans* are discussed in connection with the latter. *Sarcostemma Torreyi* inhabits dry hillsides and scrubby woodland associations in northern Mexico and southwestern Texas. It has been collected at altitudes of 4500 to 7200 feet. Judging by the relatively few specimens, it flowers from May 29 to August 18; fruits have been collected in July and September.

UNITED STATES. TEXAS: BREWSTER CO.: Chisos Mts., *Sperry 481;* PRESIDIO CO.; Fresno Canyon, N of Lajitas, *Cutler 1893.*

MEXICO. CHIHUAHUA: Sta. Eulalia Mts., *Pringle 63, 550, 1325.* COAHUILA: Muzquiz, slopes of Sierra de San Manuel, *Wynd & Muller 331;* Parras, *Purpus 4679, Stanford, Retherford & Northcraft 164;* Cuatro Ciénagas, Sierra de la Madera, *Muller 3168;* Sierra de la Gloria, SE Monclova, *Marsh 1915;* Sierra de Sta. Rosa, S of Muzquiz, *Marsh 1413.* DURANGO: Inde, *Reko 5259.* NUEVO LEON: Dulces Nombres, *Meyer & Rogers s. n.;* Monterrey, *Muller 248.* TAMAULIPAS: Cerro Tinaja, near San José, *Bartlett 10318,* type of *F. vesiculare* Woods.; 22 km. SE of Miquihuana, *Stanford, Retherford & Northcraft 869.*

10. SARCOSTEMMA CYNANCHOIDES Decne. in DC. Prodr. 8:540. 1844.

KEY TO THE SUBSPECIES

a. Leaves broadly lanceolate, 3–4 times as long as broad, cordate (rarely truncate) at the base; flowers white, the corona vesicles widest above the middle ..... 10a. *S. cynanchoides* ssp. *cynanchoides*

aa. Leaves narrowly lanceolate, more than 3–4 times as long as broad, hastate (rarely truncate or obtuse); flowers purple or pink, or the corolla lobes with a median purple streak, the corona vesicles widest below the middle ..... 10b. *S. cynanchoides* ssp. *Hartwegii*

10a. SARCOSTEMMA CYNANCHOIDES Decne. ssp. **cynanchoides** (Decne.) R. Holm, stat. nov.

Sarcostemma cynanchoides Decne. in DC. Prodr. 8:540. 1844. (T.: *Berlandier 2324 in Herb. Paris*!).
Philibertia cynanchoides (Decne.) Gray, in Proc. Amer. Acad. 12:64. 1877.
Philibertia cynanchoides var. *subtruncatum* Robins. & Fern. in Proc. Amer. Acad. 30:119. 1894. (T.: *Hartmann 4 in Herb. U. S. Nat. Mus.*!).
Philibertella cynanchoides (Decne.) Vail, in Bull. Torr. Bot. Club 24:307. 1897.
Funastrum cynanchoides (Decne.) Schltr. in Fedde's Repert. 13:284. 1915.
Funastrum cynanchoides var. *subtruncatum* (Robins. & Fern.) Macbr. in Contr. Gray Herb. n. s. 49:51. 1917.

Stems twining or trailing, green to gray-green, glabrous to sparsely puberulent; lateral branches many. Leaves broadly ovate-lanceolate, acuminate to acute, cordate, rarely truncate or somewhat hastate, the lobes usually diverging, 2–3 cm. long, 0.5–3.0 cm. wide, membranaceous, sparsely puberulent on both surfaces, with one or more glands on the midrib at the base; petiole 0.9–1.5 cm. long. Inflorescences umbelliform, 12- to 20-flowered; peduncle 3.5–4.0 cm. long, glabrescent; bracts linear, minute; pedicels slender, 1.5–1.7 cm. long, minutely pilosulose. Calyx lobes ovate, 2–3 mm. long, pilosulose without, glabrous within; squamellae absent, solitary, or paired. Corolla rotate-subcampanulate, greenish-white, rarely pinkish, the tube 2 mm. long, the lobes ovate, acute, 6–7 mm. long, glabrescent without, glabrous within, more or less ciliolate. Gynostegium 2 mm. high, the column about 0.5 mm. long. Anthers 1 mm. long, the apical appendage suborbicular, the pollinium-sacs oblongoid-cylindrical, 0.6 mm. long, with sagittate corpusculum; ring of the corona thin, revolute, not adnate to the base of the corona vesicles; vesicles of the corona suboblongoid, widest above the middle, 1.5 mm. long. Ovaries 1.5 mm. long, glabrous; stigma-head convex, obscurely bilobed. Follicles fusiform, 6.5–7.2 cm. long, 1.0–1.3 cm. thick, puberulent, finely striate; seeds unequally biconvex, 7–8 mm. long, 3–4 mm. wide, minutely papillate on both surfaces, the margin serrate; coma about 3.5 cm. long.

As interpreted here, *Sarcostemma c. cynanchoides* represents the eastern subspecies of a species ranging from Oklahoma and central Texas to western Mexico and California. While it usually can be distinguished easily from the western subspecies by its broader, shorter leaves and white flowers, these differences do not appear to be sufficiently important for specific designation. *Sarcostemma c. cynan-*

choides occupies less arid habitats and shows less evidence of morphological reduction than its western relative. It also begins to flower nearly two months later. Floral differentiation between the two subspecies is not striking: *S. c. cynanchoides* has a somewhat longer column and the corona vesicles are widest above the middle in the majority of specimens. Hybridization between them appears to be rather rare (time of flowering may be a barrier), but the area of overlap of the two ranges is in Mexico where few specimens have been collected. The nature of the cline is further discussed in connection with *Sarcostemma c. Hartwegii* (10b).

Sarcostemma c. cynanchoides has been found climbing trees and shrubs in the sandy soil of rivers and ditches and in rocky canyons; it grows at altitudes of 1600 to 6400 feet. Blooming dates range from May to September and fruit have been collected in August and September.

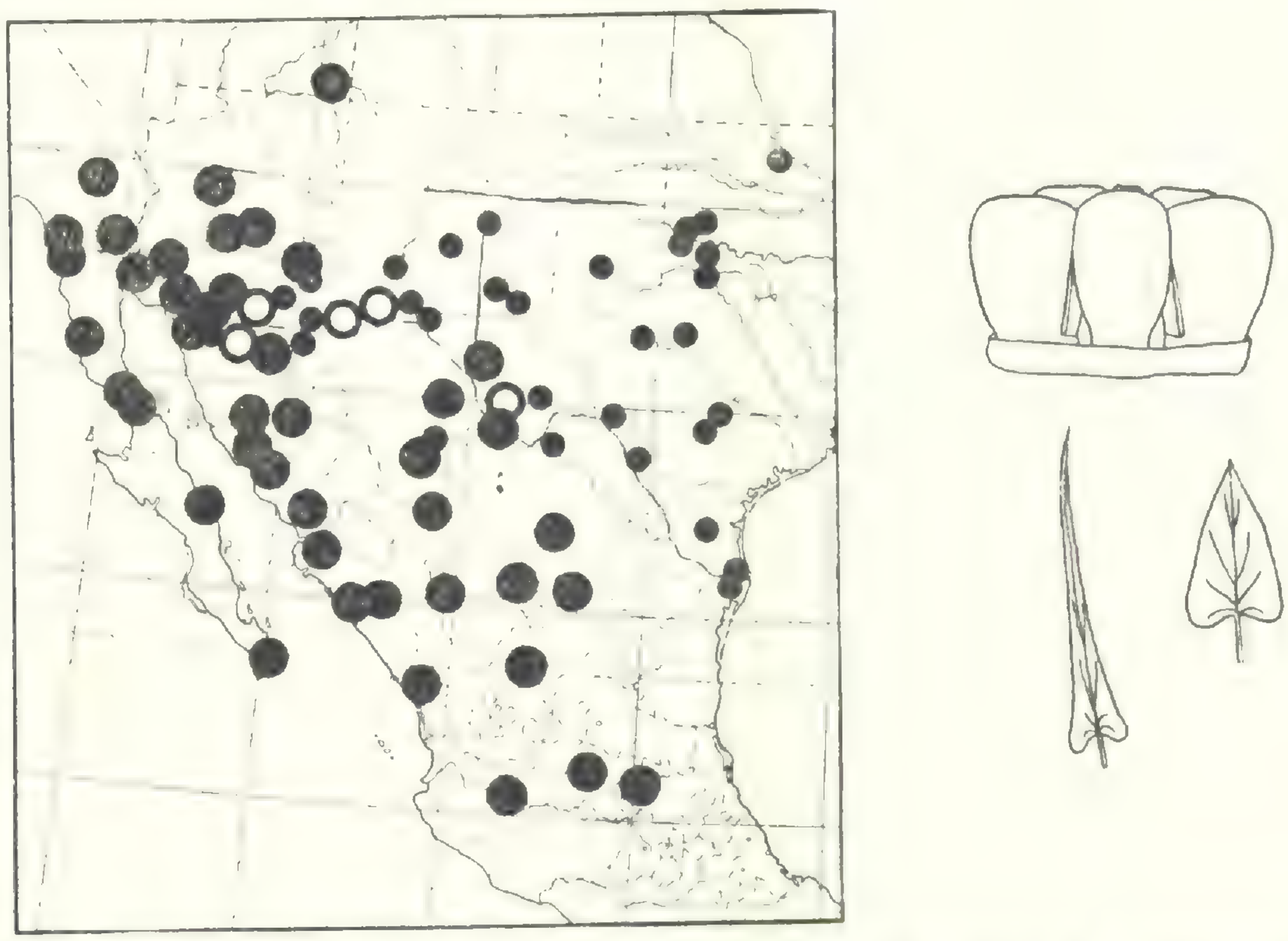

Fig. 13. Distribution of *S. cynanchoides cynanchoides* (small dots), of *S. cynanchoides Hartwegii* (large dots), of putative hybrids (black circles). Gynostegium of *S. cynanchoides* spp. (upper right); leaf of *S. cynanchoides Hartwegii* (lower left), of *S. cynanchoides cynanchoides* (lower right).

UNITED STATES. OKLAHOMA: COMANCHE CO.: Fort Sill, *Clemens 11734;* PAYNE CO.: Ripley, *Stratton 237;* TELLMAN CO.: S of Davidson, *Goodman 2266.* TEXAS: ARCHER CO.: Kickapoo Creek, *Reverchon 602;* BEXAR CO.: San Antonio, *Wilkinson s. n.;* BREWSTER CO.: Chisos Mts., *Tharp 3650;* BROWN CO.: Jim Ned Creek, *Reverchon s. n.;* CAMERON CO.: Brownsville, *Schulz 2094;* COMAL CO.: New Braunfels, *Lindheimer 993;* DUVAL CO.: Pena, *Nealley 375;* EL PASO CO.: El Paso, *Stearns 125;* HALL CO.: Estelline, *Reverchon 3875;* LUBBOCK CO.: Slaton, *Reed 3228;* MAVERICK CO.: Eagle Pass, *Havard s. n.;* TOM GREEN CO.: *Soulard s. n.;* VALVERDE CO.: Devil's River, *Eggert s. n.;* WILBARGER CO.: Vernon, *Ferris & Duncan 3352;* YOUNG CO.: Graham, *Reverchon 3199.* NEW MEXICO: CHAVES CO.: Roswell, *Earle & Earle 242;* DONA ANA CO.: Mt. Selden, *Rusby 261;* EDDY CO.: Dark Cañon, 45 miles SW of Carlsbad, *Grassl 98;* GUADALUPE CO.: Sta. Rosa, *Arsène & Benedict 16950;* LINCOLN CO.: above Tularosa, *Wooton & Standley s. n.;* LUNA CO.: Florida Mts., *Mulford 1041a;* SIERRA CO.: Animas Creek, *Metcalfe 1128.* ARIZONA: COCHISE CO.: Bisbee, *Mearns 879;* GRAHAM CO.: Clifton, *Hough s. n.;* PIMA CO.: Tucson, *Kearney & Peebles 14989.*

Mexico. CHIHUAHUA: Rio Carmen, N of Chihuahua, *Wislizenus 105;* Paso del Norte, *Pringle 1324;* Sta. Eulalia Plains, *Wilkinson s. n.* COAHUILA: Matamoros, *Berlandier 2324,* type of *S. cynanchoides* Decne., *904, 2334;* Del Carmen Mts., *Marsh 840.* NUEVO LEON: El Carrizo, *Pringle 13117;* Río Brazo del Norte, *Schott s. n.* SONORA: Fronteras, *Hartmann 4,* type of *P. c.* var. *subtruncatum* Robins. & Fern., *984, 985;* Guadalupe Canyon, *Merton 2053.*

10b. Sarcostemma cynanchoides Decne. ssp. **Hartwegii** (Vail) R. Holm, stat. nov.

Sarcostemma lineare Decne. ex Benth. Pl. Hartw. 25. 1840, non Sprengel. (T.: *Hartweg 217*!).

Sarcostemma heterophyllum Engelm. sensu Torr. in Bot. Mex. Bound. Surv. 162. 1859, as to specimens cited, not as to type.

Philibertia linearis (Decne.) Gray, Proc. Amer. Acad. 12:64. 1877.

Philibertia linearis var. *heterophylla* (Engelm. sensu Torr.) Gray, Syn. Fl. 2^1:88. 1878, as to description, not as to type.

Philibertella Hartwegii Vail, in Bull. Torr. Bot. Club 24:308. 1897, based on *S. lineare* Decne.

Philibertella Hartwegii heterophylla (Engelm. sensu Torr.) Vail, loc. cit. 1897, as to specimens cited, not as to type.

Philibertella heterophylla (Engelm. sensu Torr.) Cocker. in Bot. Gaz. 26:279. 1898, based on *P. Hartwegii heterophylla* (Engelm. sensu Torr.) Vail.

Funastrum Hartwegii (Vail) Schltr. in Fedde's Repert. 13:285. 1914.

Funastrum lineare (Decne.) Macbr. in Contr. Gray Herb. n. s. 49:50. 1917.

Funastrum lineare var. *heterophyllum* (Engelm. sensu Torr.) Macbr. loc. cit. 1917, based on *P. Hartwegii heterophylla* (Engelm. sensu Torr.) Vail.

Funastrum heterophyllum (Engelm. sensu Torr.) Standl. in Contr. U. S. Nat. Herb. 23:1170. 1924, as to description, not as to type.

Philibertia heterophylla (Engelm. sensu Torr.) Jepson, Man. Fl. Pl. Calif. 770. 1925, as to description, not as to type.

Stems twining or trailing, green, glabrate to puberulent, the nodes white puberulent; lateral branches many. Leaves narrowly lanceolate, acuminate, hastate, or cordate, sometimes obtuse, the lobes diverging, 1–11 cm. long, 0.1–2.5 cm. wide, membranaceous, glabrate to subpuberulent on both surfaces, with one or more glands on the midrib at the base; petiole 0.9–1.9 cm. long. Inflorescences umbelliform, 7- to 14-flowered; peduncle slender, 0.5–5.5 cm. long, pilosulose; bracts linear, minute; pedicels slender, 0.7–1.5 cm. long, puberulent. Calyx lobes ovate-linear, 2–3 mm. long, pilosulose without, glabrous within; squamellae usually solitary. Corolla rotate-subcampanulate, purple to pink, or the lobes each with a median purple streak, the tube 1 mm. long, the lobes ovate, acuminate to acute, 5–7 mm. long, puberulent without, glabrous within, ciliolate. Gynostegium 2.5 mm. high, the column very short. Anthers 1 mm. long, the apical appendage suborbicular, the pollinium-sacs oblongoid-cylindrical, with ellipsoid-sagittate corpusculum; ring of the corona prominent, not adnate to the base of the corona vesicles; vesicles of the corona rectanguloid, widest below the middle, 1.5 mm. long. Ovaries 1.5 mm. long, glabrous; stigma-head convex, obscurely bilobed. Follicles slender, fusiform, attenuate, 7.4–11.0 cm. long, 0.6–1.0 cm. thick, minutely puberulent, finely striate; seeds unequally biconvex, 6 mm. long, 1.5 mm. wide, minutely rugose dorsally, minutely papillate ventrally; coma about 3.5 cm. long.

The taxonomy of this subspecies and of S. *crispum* is confused by the widespread misapplication of the name S. *heterophyllum* Torr. In 1859, Torrey published this manuscript name of Engelmann, citing but one specimen, *Wright 1679*, which must be regarded as the type. This specimen, however, is an example of S. *crispum* with very narrow leaves in which crisping or undulation is not apparent. Two years later, Torrey referred *Wright 1681* of the Mexican Boundary Survey collections to S. *heterophyllum*. This specimen proves to be S. *cynanchoides Hartwegii* and the description given by Torrey clearly applies to that subspecies. All later authors have followed this misapplication of the name in making various combinations in *Philibertia, Philibertella,* and *Funastrum*.

Inasmuch as the type of the first-published S. *heterophyllum* actually is S. *crispum,* this name and subsequent combinations are nomenclaturally related to S. *crispum* and unavailable for the lanceolate-leaved subspecies of S. *cynanchoides*. The epithet *lineare* also is pre-empted by the earlier name of Sprengel. I have preferred to employ *Hartwegii,* rather than coin a new name, despite the fact that, owing to this early misunderstanding, it never was used widely.

Sarcostemma c. Hartwegii is similar to the eastern subspecies in most respects, differing in the narrower, longer leaves and purple flowers. Intergradation between the two forms appears to be uncommon, but occurs in a narrow northwest-southeast belt from Arizona to central Mexico. Hybridization has produced an abruptly stepped cline and intermediate forms have been designated as S. *c.* cl. *cynanchoides-Hartwegii*.

In contradistinction to S. *c. cynanchoides,* S. *c. Hartwegii* usually grows in dry, sandy or rocky soil of arroyos and plains. Occasionally it is found in cultivated bottom lands and ditches, in which case the flowers are larger and the leaves often fully ten times as large as normal. The altitudinal range is from 100 to 5000 feet, overlapping that of the eastern subspecies. Flowering specimens have been collected from February to early September, this season beginning about two months before that of S. *c. cynanchoides*. Fruiting specimens dated from April to October have been seen.

UNITED STATES. UTAH: SAN JUAN CO.: 6 miles above mouth of San Juan River, *Cutler 3180;* Forbidding Canyon, near Colorado River, *Cutler 2831*. TEXAS: BREWSTER CO.: Chisos Mts., *Muller 8117;* CULBERSON CO.: near Van Horn, *Waterfall 5447;* PRESIDIO CO.: Presidio, *Havard s. n.* NEW MEXICO: DONA ANA CO.: mesa W of Organ Mts., *Standley s. n.;* LUNA CO.: Florida Mts., *Mulford 1063*. ARIZONA: GILA CO.: Collom Camp, Matzatzal Mts., *Collom 6;* GRAHAM CO.: near Safford, *Maguire 10931;* PIMA CO.: near Sta. Rosa, *Cutler 4724;* PINAL CO.: near Mammoth, *Peebles 14611;* MARICOPA CO.: 23 miles N of Phoenix, *Gillespie 8660;* YAVAPAI CO.: near Congress Junction, *Gillespie 8502*. CALIFORNIA: IMPERIAL CO.: near Ogilby, *Alexander & Kellogg 1951;* LOS ANGELES CO.: Covina, *G. B. Grant 972;* RIVERSIDE CO.: Snow Creek Canyon, San Jacinto Mts., *Munz 12397;* SAN BERNARDINO CO.: San Bernardino Valley, *Parish & Parish 309;* SAN DIEGO CO.: Box Canyon, *Munz & Hitchcock 12048*.

MEXICO. BAJA CALIFORNIA NORTE: Punta Prieta, *Wiggins 7738;* 30 miles N of Punta Prieta, *Wiggins 5346;* San Quintín Bay, *E. Palmer 639;* 14.5 miles E of Agua Caliente, *Keck 1925*. BAJA CALIFORNIA SUR: Mulege, *Johnston 3684;* Santa Agueda, *E. Palmer 231;* near San José del Cabo, *Wiggins 5682*. CHIHUAHUA: Bachimpa, S of Chihuahua, *Wislizenus 255;* near Chihuahua, *E. Palmer 84, Pringle 1051;* Sta. Eulalia Plains, *Wilkinson*

s. n.; 5 miles E of Allende turn-off, road Parral-Camargo, *Freytag & Baxter 65*. COAHUILA: Movans, *Purpus 4485*; 10 miles N of Cuatro Ciénegas, *Wynd 738*; near Parras, *Shreve 8761*; Torreon, *Pittier 505*. DURANGO: Santiago Papaquiaro, *Nelson 4661, E. Palmer 39*. GUANAJUATO: Guanajuato, *Duges 7*. JALISCO: near Guadalajara, *Pringle 5885, 8497, 11628, Safford 1426*. QUERÉTARO: near San Pablo, *Rose, Painter & Rose 9817*; between Huiguerilla and San Pablo, *Altamirano 7702*. SINALOA: San Blas, *M. E. Jones 23249*; Villa Union, *Lamb 445*; Altata, *Rose 1375*; Culiacán, *Partidas 2015, 2016*; San Ignacio, *Montes & Salazar 53*; near Fuerte, *Rose, Standley & Russell 13928*; near Villa Union, *Rose, Standley & Russell 14639*. SONORA: Cocorit, Yaqui Valley, *Gentry 888*; San Bernardo, Río Mayo, *Gentry 1308*; 5.7 miles NW of Caborca, *Wiggins 8265*; near Suhuoral, *Wiggins & Rollins 264*; 24 miles SW of Sonoyta, *Shreve 7588*; 35.3 miles SW of Sonoyta, *Wiggins 8363*; near Guaymas, San Carlos Bay, *Ferris 8730*; Rancho San Ignacio, 10 miles N of Vicam, *Wiggins 6461*; Forin, *Studhalter 1370*; near Cucurpe, *Wiggins 7170*; Hermosillo, *Maltby 198*; Alamos, *Goldman 307*; Pitequito, *Kennedy 7080, Keck 4014*; near Altar, *Long 10*; near Magdalena, *Rose, Standley & Russell 15065*; Realito, 10 miles E of Altar, *Shreve 6371*; Navajoa, *Rose, Standley & Russell 13134*; 20 miles N of Sargento, *Mallery & Turnage s. n.* ZACATECAS: Cedros, *Lloyd 123*.

SARCOSTEMMA CYNANCHOIDES cl. CYNANCHOIDES-HARTWEGII.

UNITED STATES. TEXAS: PRESIDIO CO.: 24 miles S of Marfa, *Hinckley 1051*. NEW MEXICO: HIDALGO CO.: Virdin, *Hershey A-11*; LUNA CO.: Florida Mts., *Mulford 1041a*. ARIZONA: PIMA CO.: Rincon Mts., *Harrison & Kearney 5820*.

MEX.CO. SONORA: along Río de los Alisos, 31 miles S of Nogales, *Wiggins 7034A*.

11. SARCOSTEMMA **hirtellum** (A. Gray) R. Holm, comb. nov.

Sarcostemma heterophyllum Engelm. sensu Torr. var. *hirtellum* Gray, in Brewer & Watson, Bot. Calif. 1:178. 1876. (T.: *Cooper s. n.*!).
Philibertia linearis (Decne.) Gray, var. *hirtella* Gray, Syn. Fl. 2[1]:88. 1878.
Philibertella hirtella (Gray) Vail, in Bull. Torr. Bot. Club 24:309. 1897.
Philibertia hirtella (Gray) Parish, in Muhlenbergia 3:126. 1907.
Funastrum hirtellum (Gray) Schltr. in Fedde's Repert. 13:286. 1915.

Stems twining, trailing, or semi-erect, gray-green, densely canescent; lateral branches many. Leaves linear to narrowly lanceolate, acuminate to acute, obtuse, rarely truncate, 1.0–3.6 cm. long, 0.1–0.5 cm. wide, pilosulose on both surfaces, coriaceous, without glands on the midrib; petiole 0.1–1.5 cm. long. Inflorescences umbelliform, 9- to 12-flowered; peduncle 1.5–4.9 cm. long, pilosulose; bracts linear, minute; pedicels 0.6–0.9 cm. long, pilosulose. Calyx lobes linear, 2.0–2.5 mm. long, densely subpilose on both surfaces; squamellae absent or solitary. Corolla rotate-subcampanulate, white, the tube 1 mm. long, the lobes ovate-lanceolate, acute, 4–5 mm. long, glabrous without, subpilose within, ciliolate. Gynostegium 2 mm. high, the column about 0.5 mm. long. Anthers 0.75 mm. long, the apical appendage ovate-elliptic, the pollinium-sacs somewhat flattened, 0.5 mm. long, with ellipsoid to narrowly sagittate corpusculum; ring of the corona thin, adnate to the base of the corona vesicles; vesicles of the corona oblongoid, 1.5 mm. long. Ovaries 1.5 mm. long, essentially glabrous; stigma-head slightly convex, obscurely bilobed. Follicles paired, narrowly fusiform, grayish-yellow, waxy, 3.8–4.7 cm. long, 0.3–0.5 cm. thick, very minutely but thickly puberulent; seeds somewhat flattened, 8 mm. long, 4 mm. wide, rugose-papillate dorsally, minutely papillate ventrally; coma about 2.5 cm. long.

Sarcostemma hirtellum has a restricted distribution in the Colorado and Mojave deserts in Nevada, California, and Arizona. It has been confused in the herbarium with S. *cynanchoides Hartwegii* from which it differs in the narrow, pubescent leaves, canescent aspect, and semi-erect habit, in addition to important, though less prominent, floral differences. In contradistinction to all other species in the New World, S. *hirtellum* appears invariably to have paired follicles which diverge markedly from one another. The species probably is most closely related to the western subspecies of S. *cynanchoides*, but must be considered a species on morphological criteria.

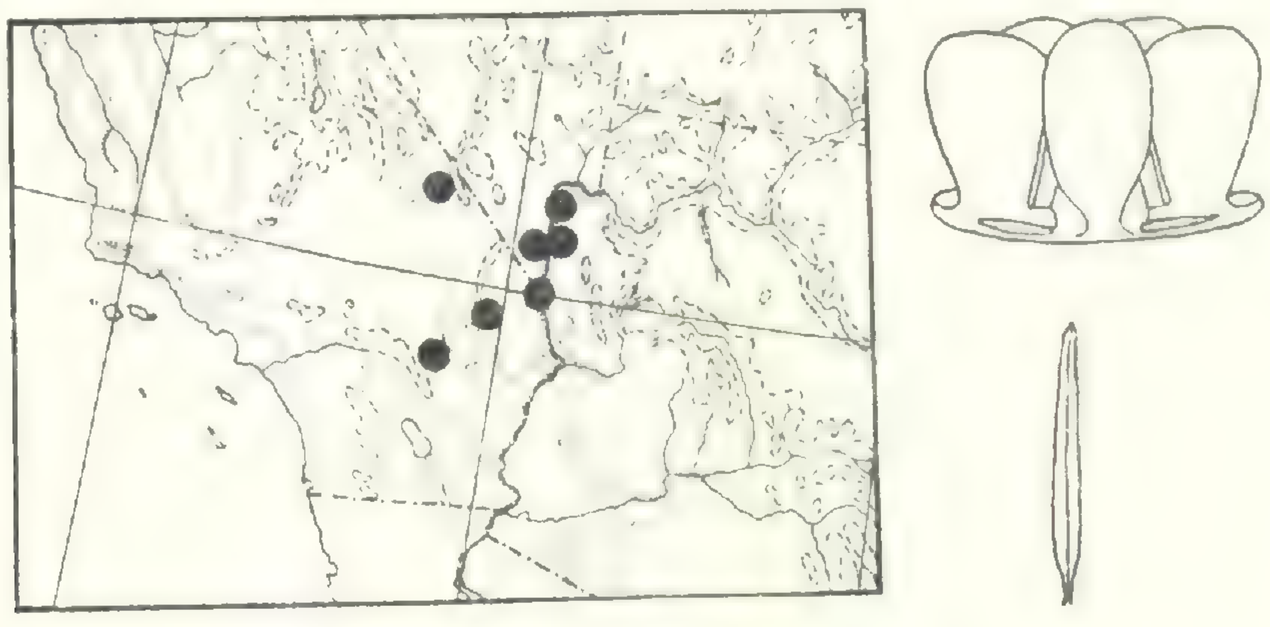

Fig. 14. Distribution, gynostegium, and leaf of S. *hirtellum*.

Sarcostemma hirtellum occurs at altitudes of from 450 to 3500 feet. It is an undershrub several feet in height, but creeping branches may extend several feet along the sandy or rocky soil of the ravines of washes in which it grows. While the aerial stems are slender and herbaceous, there is a large, woody caudex at the base and a series of very stout, deeply penetrating roots. The crushed herbage has an odor pronouncedly sudoral or reminiscent of garlic. Blooming dates range from March 26 to May 5; one specimen was collected in flower in October. Follicles are produced from April to May.

UNITED STATES. NEVADA: CLARK CO.: 14 miles E of Searchlight, *Train 1283;* Mike Tobins, *Thackery 333*. ARIZONA: MOHAVE CO.: 7 miles S of Boulder Dam, *Peebles & Parker 14785;* YUMA CO.: Buckskin Mts., *Keck 4345*. CALIFORNIA. CALAVERAS CO.: Vallecito, *Orcutt 2250;* RIVERSIDE CO.: Corn Springs, *C. L. Hitchcock 12199;* SAN BERNARDINO CO.: near Needles, *Macbride & Drouet 4453;* SAN DIEGO CO.: San Felipe Canyon, *Eastwood 2780*.

12. SARCOSTEMMA ARENARIUM Decne. ex Benth. Bot. Voy. Sulph. 34. 1844. (T.: *Hinds 1841 in Herb. Kew.*!).

Stems twining or trailing, very thick at the base and with much ridged bark, gray-green above, puberulent, the nodes densely white-pubescent; lateral branches many and long at the base, few above. Leaves more or less caducous, narrowly oblanceolate, obtuse, cuneate, 3.5 cm. long, 0.3–0.8 cm. wide, coriaceous, somewhat revolute when dried, sparsely pilose above and beneath with small glands on the midrib at the base; petiole 0.05–0.1 cm. long. Inflorescences umbelliform, 6- to 12-flowered; peduncle 2.2–3.5 cm. long, rarely equalling the subjacent inter-

node in thickness, pilose; bracts linear, 0.1–0.2 cm. long; pedicels 1.0–1.3 cm. long, densely pilose. Calyx lobes narrowly lanceolate, 3 mm. long, involute, pilose without, glabrous within; squamellae alternate, usually solitary, relatively long. Corolla rotate-subcampanulate, the tube 2.5–3.0 mm. long, the lobes ovate, obtuse, 4.5–6.0 mm. long, pilose without, puberulous-papillate within, ciliate. Gynostegium 2.5–3.0 mm. high, the column 1 mm. long. Anthers 1 mm. long, the apical appendage deltoid, the pollinium-sacs clavate-oblongoid, 0.5 mm. long, with narrowly sagittate corpusculum; ring of the corona prominent, somewhat revolute, adnate to the column; vesicles of the corona spherical to oblongoid, 1.0–1.5 mm. long. Ovaries 2 mm. long, rather densely pilose; stigma-head obscurely bilobed, convex. Follicles narrowly obclavate, attenuate, 6.4 cm. long, 0.9 cm. thick, puberulent; seeds unequally biconvex, 7 mm. long, 3 mm. wide, obscurely rugose dorsally, minutely papillate ventrally; coma about 3 cm. long.

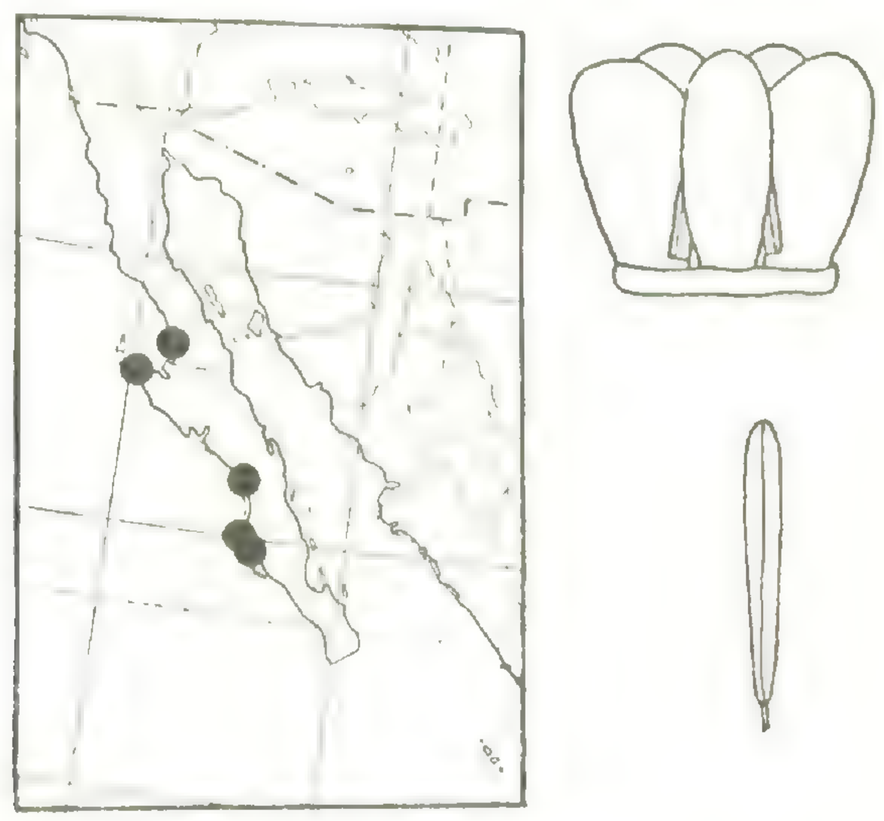

Fig. 15. Distribution, gynostegium, and leaf of *S. arenarium*.

A poorly understood species endemic to the western coast of Baja California. *Sarcostemma arenarium* has been confused with *S. cynanchoides Hartwegii* and *S. hirtellum*, from both of which, however, it is rather easily distinguished by its oblanceolate leaves, larger flowers, and densely pubescent calyx. In many respects it is fairly close to *S. clausum*, and may perhaps represent an offshoot of that variable stock. If so, it has diverged so far in the direction of ser. CYNANCHOIDES as to make any statements concerning its relationships very tenuous.

MEXICO. BAJA CALIFORNIA SUR: San Bartolomé Bay, *Rose 16214;* Magdalena Bay, *Mason 1029, Hinds 1841,* TYPE; Magdalena Island, *Orcutt 31, Brandegee 1889;* Lagoon Head, *E. Palmer 814;* San Juanico, *Gentry 4297.*

Series 4. ANGUSTISSIMA R. Holm, ser. nov.

Inflorescentia vere terminalis umbelliformis, pedunculo quam internodio subjacenti angustiore (interdum obsoleto).

Type species: *Sarcostemma angustissimum* (Anderss.) R. Holm.

This monotypic series includes a single species, endemic to the Galapagos Islands, which differs from other members of the genus in having a truly terminal inflorescence.

13. SARCOSTEMMA **angustissimum** (Anderss.) R. Holm, comb. nov.

Asclepias angustissima Anderss. Galap. Oarnes Veg. 196. 1853. (T.: *Andersson s. n. in Herb. Stockholm*!).
Funastrum angustissimum (Anderss.) Fourn. in Ann. Sci. Nat. Bot. VI, 19:388. 1882.

Stems twining or semi-erect, green, glabrous; lateral branches many. Leaves oblanceolate, linear, acute, cuneate, 2.5–4.5 cm. long, 0.1–0.3 cm. wide, subcoriaceous, revolute when dried, glabrous above and beneath, without glands on the midrib at the base; petiole 0.1–0.2 cm. long. Inflorescences umbelliform, terminal to the main axis or lateral branches, 7- to 15-flowered; peduncle 0–1 cm. long, very minutely pilosulose, not equalling the subjacent internode in thickness; bracts linear, minute; pedicels 0.5–1.5 cm. long, very minutely pilosulose. Calyx lobes ovate, 1.5 mm. long, hispidulous without, glabrous within, ciliolate, the apex glandular; squamellae absent. Corolla rotate-subcampanulate, black when dried, the tube 1.25 mm. long, the lobes ovate, acute, 2.5 mm. long, glabrous on both surfaces. Gynostegium 2 mm. high, the column very short. Anthers 1 mm. long, the apical appendage semi-orbicular, the pollinium-sacs oblongoid, 0.5 mm. long, with sagittate corpusculum; ring of the corona thin, scarcely adnate to the base of the corona vesicles; vesicles of the corona ovoid-oblongoid, pointed at the tip, 2 mm. long. Ovaries 1 mm. long, very minutely pubescent; stigma-head convex, entire. Follicles apparently narrowly fusiform, about 9 (?) cm. long; seeds unknown.

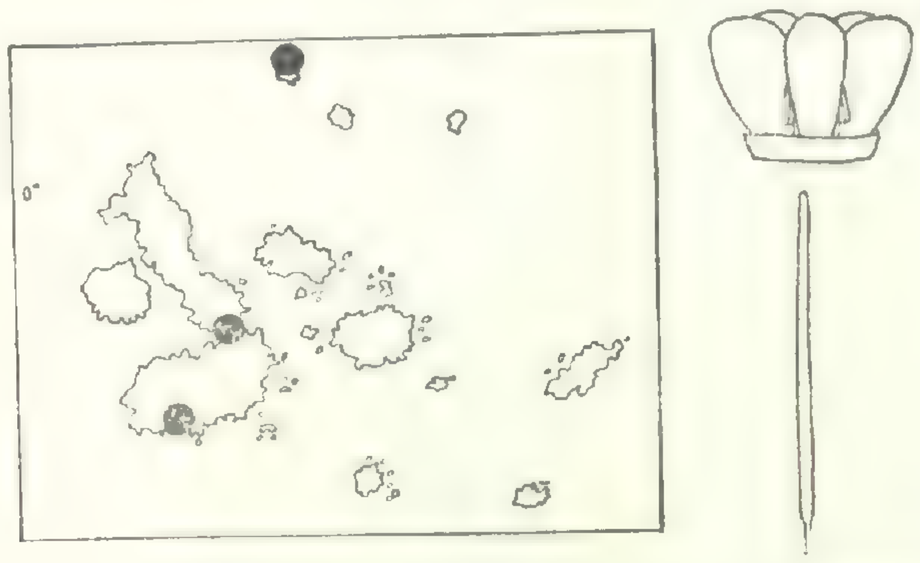

Fig. 16. Distribution, gynostegium, and leaf of S. *angustissimum*.

The small, dark flowers of this Galapagos Island endemic are quite distinctive, as are the terminal inflorescences. Little can be said about the relationships of S. *angustissimum* since it has been so rarely collected and is so reduced morphologically. Apparently it flowers from January to June.

GALAPAGOS ISLANDS. ABINGDON IS.: *Snodgrass & Heller 845*. ALBEMARLE IS.: *Andersson s. n.*, TYPE; Tagus Cove, *Snodgrass & Heller 145*.

Series 5. FLAVA R. Holm, ser. nov.

Coronae annulus obsoletus.

Type species: *Sarcostemma flavum* Decne.

A monotypic series including a species of the Río de la Plata area of South America. The ring of the corona is entirely lacking, immediately separating this species from all others in the subgenus.

14. SARCOSTEMMA FLAVUM Decne. in DC. Prodr. 8:540. 1844. (T.: *D'Orbigny s. n. in Herb. Paris.*!).

Philibertia stellaris Griseb. Symb. Fl. Arg. 234. 1879, ex char.
Cystostemma umbellatum Fourn. in Mart. Fl. Bras. 6^4:204. 1885. (T.: *St. Hilaire s. n.*!).
Ceramanthus flavus (Decne.) Malme in Ark. Bot. 4^{14}:2. 1905.
Philibertia longifolia Arech. in Ann. Mus. Nac. Montevideo 4:87. 1909, ex char.
Funastrum flavum (Decne.) Malme, in Bull. Soc. Bot. Genève. II, 3:269. 1911.
Funastrum longifolium (Arech.) Schltr. in Fedde's Repert. 13:286. 1915.

Stems twining, green, pilosulose; lateral branches few. Leaves long, lanceolate, acuminate to acute, cordate, the lobes descending, 7.0–12.5 cm. long, 3.5–4.0 cm. wide, subcoriaceous, appressed-pilose above, densely so beneath, with several glands on the midrib at the base; petiole 1.5–2.0 cm. long. Inflorescences umbelliform, the floriferous axis slightly manifest, 9- to 15-flowered; peduncle 4.5–14.0 cm. long, pilosulose; bracts linear, minute; pedicels 5–10 cm. long, pilose. Calyx lobes narrowly lanceolate, 2.5 mm. long, copiously puberulent without, glabrous within; squamellae 3–7, alternate. Corolla rotate-subcampanulate, the tube 0.9 mm. long, the lobes broadly ovate, 4 mm. long, glabrescent without, glabrous within. Gynostegium 2.5 mm. high, the column obsolete. Anthers 1.5 mm. long, the apical appendage deltoid, obscurely emarginate, the pollinium-sacs oblongoid-cylindrical, 0.5 mm. long, with ellipsoid to obscurely sagittate corpusculum; ring of the corona lacking; vesicles of the corona ovoid, the inner side more or less apiculate at the tip, 2.5 mm. long. Ovaries 1.5 mm. long, glabrous; stigma-head obscurely bilobed. Follicles and seeds unknown.

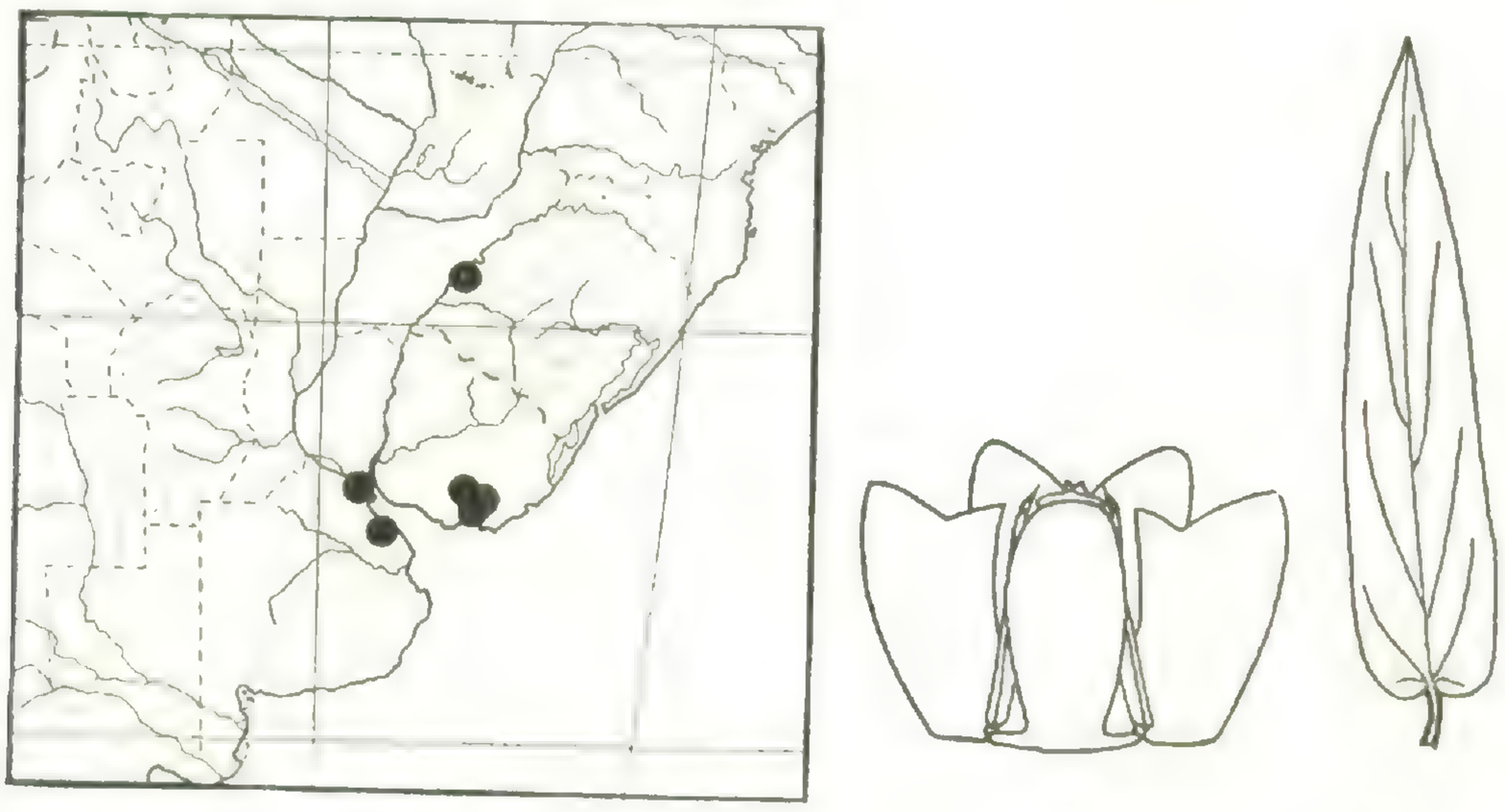

Fig. 17. Distribution, gynostegium, and leaf of *S. flavum*.

This distinctive species apparently is rare, for few specimens have been available for study. The lack of the ring of the corona and the disproportionate length of the leaves form good characters. One of the few species which occurs in lowland areas, it inhabits the borders of the Paraná and Plata rivers. Only the type specimen and the material from the Naturhistoriska Riksmuseet, Stockholm, have been available, so that most of the distribution records are taken from the monograph of the Argentine species of *Funastrum* and *Philibertia* by T. Meyer.[56] The species ranges from southern Brazil to adjacent Argentina and Uruguay.

BRASIL. RÍO GRANDE DO SUL: *St. Hilaire s. n.*, type of *C. umbellatum* Fourn.
URUGUAY. CANELONES: near the Río de la Plata, *Legrand 34*. CERRO LARGO: Cerro de las Cuentas, *Rosengurtt 2773*. SAN JOSÉ: Barra, *Herter 738*; Santa Lucía, *Arechaveleta s. n.*

ARGENTINA. BUENOS AIRES: Conchitas, orillas del Río de la Plata, *Hauman s. n.*; delta del Paraná, *Hauman s. n.* ENTRE RÍOS: Río Bravo, *Kuschel 532, 533, 534*.

Subgenus II. OXYSTELMA (R. Br.) R. Holm, stat. nov.

Oxystelma R. Br. in Mem. Wern. Soc. 1:40. 1809.
Philibertia HBK. Nov. Gen. et Sp. Pl. 3:195. 1819.
Pentagonium Schauer, in Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1:364. 1843.
Lugonia Wedd. Chlor. And. 2:49. 1857.
Zosima Phil. Sert. Mend. Alt. 29. 1871, non Hoffm.
Pentacyphus Schltr. in Engl. Bot. Jahrb. 37:605. 1906.
Tetraphysa Schltr. loc. cit. 616. 1906.

Leaves laminate; inflorescences racemiform or umbelliform; corolla subrotate-campanulate to campanulate, ring of the corona adnate to the corolla or more or less obsolete.

Type species: *Sarcostemma esculentum* (L.) R. Holm.

The species of this subgenus are South American plants of Andean affinities, except for the Old World S. *esculentum* which occurs in Africa and Asia. Because of the close similarity in vegetative structure between the various species, it has been necessary to place a greater emphasis on characters of the gynostegium in the keys. In every case, however, examination of the dried flowers should suffice for identification; drawings are provided to illustrate the typical condition for each species.

KEY TO THE SECTIONS

A. Vesicles of the corona ovoid to subspheroid, obtuse at the apex or abruptly constricted to form a short apical process, never exceeding the stigma-head in length; ring of the corona glabrous or obsolete; column glabrous; translator arms well-developed. Species of the Western Hemisphere.
B. Corolla lobes acute or acuminate, the tube free from the column (partly adnate in S. *lysimachioides*), glabrous within; gynostegium not highly vernicose, the column terete or ribbed, not deeply grooved; inflorescences racemiform or umbelliform, consisting of many 1- to 2-flowered cymules (occasionally indicated only by their bracts or reduced to one) ..... Section 1. PHILIBERTIA (Spp. 15–20)

[56] Meyer, T. In Lilloa 9:428. 1943.

BB. Corolla lobes broadly obtuse, the tube adnate to the column directly below the anthers, pubescent within forming five hairy pouches alternating with the stamens; gynostegium highly vernicose, the column longitudinally grooved between the stamens, the margins of the groove produced and arrect, continuous with the anther wings; inflorescence racemiform, consisting of 2 1-flowered cymules, or umbelliform. ... .Section 2. PENTACYPHUS (Spp. 21–22)

AA. Vesicles of the corona ovoid, gradually constricted above into a long, incurved process, exceeding the stigma-head in length; ring of the corona pubescent; column pubescent; translator arms obsolete. Species of the Eastern Hemisphere.....Section 3. EUOXYSTELMA (see p. 482)

Section 1. PHILIBERTIA (HBK.) Decne. in DC. Prodr. 8:541. 1844.

The majority of the species in the subgenus OXYSTELMA belong to this group of forms of undoubted close relationship. All appear to be more or less localized in distribution, in contrast to the species of subg. CERAMANTHUS or EUSARCOSTEMMA, except for S. *Gilliesii* of Argentina and Bolivia. As a rule, they may be recognized easily by the campanulate corolla, the glabrous gynostegium with scarcely apparent corona ring, and the few-flowered inflorescence.

KEY TO THE SPECIES

a. Plants usually climbing, very rarely semi-erect; corolla tube free from the column.

b. Corolla broadly and shallowly campanulate; vesicles of the corona equalling or somewhat exceeding the anthers (rarely reduced in aberrant individuals, cf. S. *Gilliesii*); pollinia rounded, clavate-cylindrical, fertile to the attachment of the translator arm, the corpusculum sagittate.

c. Vesicles of the corona narrowly ovoid-oblongoid, with a vertical ventral keel, gradually decurrent upon the column, the gynostegium somewhat longer than broad; sepals reflexed, corolla 2–3 cm. broad..... 15. *S. campanulatum*

cc. Vesicles of the corona truncate-oblongoid or ovoid to spheroid, not decurrent upon the column, the gynostegium usually broader than long; sepals ascending, corolla 0.8–1.0 cm. broad, rarely to 2 cm. broad.

d. Inflorescences racemiform to corymbiform, obviously compound; stigma-head usually 2-apiculate; vesicles of the corona narrowly ovoid or obovoid to subspheroid, with a more or less pronounced apical appendage, constricted at their insertion upon the column.

e. Vesicles of the corona widest below the middle, the gynostegium uniformly light in color; corolla with purple markings within..... 16. *S. Gilliesii*

ee. Vesicles of the corona widest above the middle, light in color, the column and anthers very dark; corolla usually uniformly light in color..... 17. *S. Vaileae*

dd. Inflorescences umbelliform, the pedicels all inserted at nearly the same point; stigma-head umbonate or broadly 2-lobed; vesicles of the corona truncate-oblongoid, scarcely constricted at their insertion upon the column..... 18. *S. solanoides*

bb. Corolla urceolate-campanulate; vesicles of the corona about one-third to one-half the length of the anthers; pollinia flattened, clavate, with a sterile hyaline region at the attachment of the translator arm, the corpusculum narrowly ellipsoid..... 19. *S. stipitatum*

aa. Plants prostrate, the branches trailing from a short woody caudex; corolla tube adnate to the column directly below the anthers.. ... ... 20. *S. lysimachioides*

15. SARCOSTEMMA CAMPANULATUM Lindl. Bot. Reg. n.s 9, *t. 36.* 1846. (T.: *Hort. Veitch. in Herb. Univ. Cantab.*!).

Philibertia campanulata (Lindl.) Nichols. Dict. Gard. 3:96. 1886.
Philibertia hypoleuca Schltr. in Oesterr. Bot. Zeitschr. 45:450. 1895. (T.: *Kunze s. n. in Herb. Berol.*).
Philibertia splendens Lillo, in Physis 4:429. 1919. (T.: *Lillo 7350 in Herb. Lillo*!).
Philibertia speciosa Malme, in Ark. Bot. 26A[4]:32. 1935, *sphalm.*

Stems twining, minutely pilosulose in lines decurrent from the petioles; lateral branches few. Leaves lanceolate, acuminate, rather deeply cordate, the lobes descending, 3.5–8.0 cm. long, 1.0–4.8 cm. wide, firmly membranaceous, glabrate to minutely puberulent above, subtomentose to tomentose beneath, with one or more glands on the midrib at the base; petiole 1.0–4.2 cm. long. Inflorescences racemiform, 2- to 9-flowered; peduncle 0.7–7.8 cm. long, appressed-pilosulose; bracts linear, 0.2–0.3 cm. long; pedicels 1.1–2.4 cm. long, appressed-pilosulose. Calyx lobes narrowly lanceolate, reflexed, 4 mm. long, puberulous-pilose on both surfaces; squamellae few, alternate. Corolla campanulate, greenish yellow to cream with red or purple spots or streaks within, the tube 8 mm. long, the lobes acute to acuminate, 5 mm. long, pilosulose without, glabrous within. Gynostegium 5–6 mm. high, the column 2 mm. long. Anthers 1.5 mm. long, the apical appendage deltoid, the pollinium-sacs clavate-cylindrical, 0.5 mm. long, with broadly sagittate corpusculum; ring of the corona very short; vesicles of the corona narrowly oblongoid, the ventral face constricted longitudinally to form a vertical keel, gradually decurrent upon the column, 2 mm. long (rarely much reduced). Ovaries 2 mm. long, sparsely puberulent; stigma-head cylindrical, with a long 2- or 3-fid apiculation. Follicles and seeds unknown.

Sarcostemma campanulatum is distinguished from all other species of the genus by the structure of the gynostegium. Here the corona vesicles are constricted longitudinally along the ventral face so that a vertical ventral keel is produced; there is no terete appendage such as is found in many species. Dorsally, the corona vesicles are decurrent upon the column to the corolla. It is noteworthy that the anther wings are usually broad and cartilaginous, while the pollinia are stout and short and connected by broad, sagittate corpuscula. A peculiar variant, which has been collected several times in the Cuzco region in Peru, has corona vesicles which are shrunken and more or less linear in outline. The gynostegium nevertheless is clearly that of *S. campanulatum*. As a rule in this form, the leaves are decidedly more tomentose beneath and the sepals are less strongly reflexed.

It is by virtue of the long, racemiform inflorescence and relatively unbranched habit, coupled with the large size, that *S. campanulatum* is assigned the primary position in the section. The relationships in subg. OXYSTELMA are, in general, much less clear than those in subg. CERAMANTHUS, so that this position in the sequence of species is based primarily on the general impression given by the plant, rather than upon any rigorous or dogmatic treatment of morphological criteria.

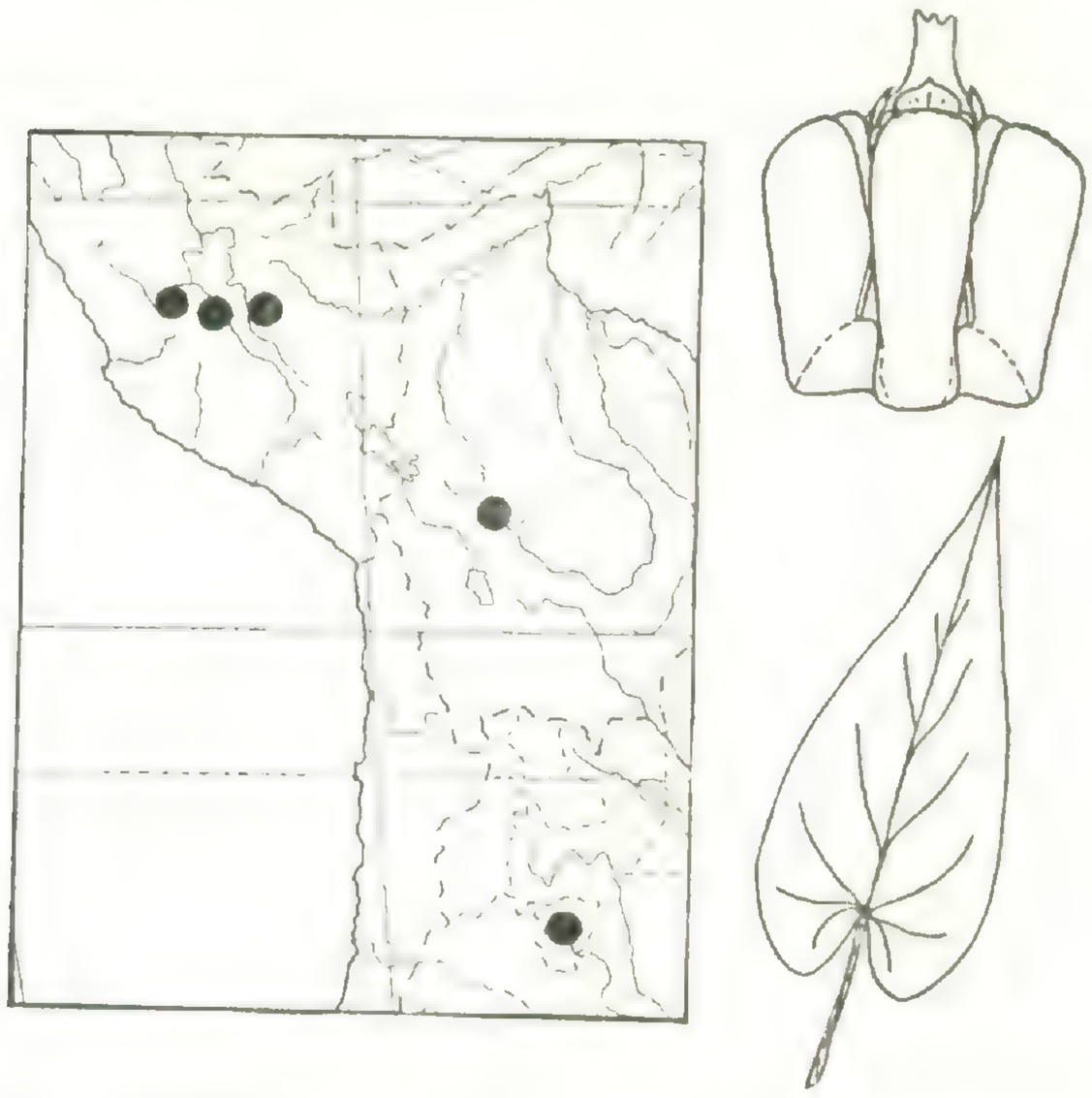

Fig. 18. Distribution, gynostegium, and leaf of *S. campanulatum*.

Sarcostemma campanulatum is a stout vine climbing to heights of four meters in small trees and shrubs. Apparently it grows in relatively moist locations in woods and occasionally in cultivated ground, at altitudes from 6000 to 11000 feet in the Peruvian and Bolivian Andes. The specimens from Tucumán, Argentina, are rather inexplicable. The species has been collected in flower from December to March, and in fruit in April.

Peru. apurimac: Abancay, Labrama, Matara Canyon, *Vargas 9801;* Abancay, Ampuy, *Stork, Horton & Vargas 10953;* Abancay, Labrama, *Vargas 1426;* Abancay, Mariño, *Vargas 1459.* cuzco: Anta, *Vargas 204;* Colca, Vilcabamba, *Vargas 4013;* Paruro, entre Huachachacca i Huanca-Huanca, *Vargas 2387.* huancavelica: Tayacaja, Ampurco, *Weberbauer 6503;* Tayacaja, 3 km. N of Salcabamba, *Stork & Horton 10318.*

Bolivia. cochabamba: Tunari, *Kuntze s. n.*, type of *P. hypoleuca* Schltr.

Argentina. tucumán: Tafí, La Angostura, *Castillón 2034;* Chicligasta, Estancia Las Pavas, *Venturi 6458.*

16. Sarcostemma Gilliesii (H. & A.) Decne. in DC. Prodr. 8:542. 1844.

Philibertia Gilliesii Hook. & Arn. in Hook. Lond. Jour. Bot. 1:290. 1834. (T.: *Tweedie s. n. in Herb. Kew.*!).

Philibertia grandiflora Hook. in Bot. Mag. 64, *t. 3618.* 1837. (T.: *Tweedie s. n. in Herb. Kew.*!).

Philibertia gracilis D. Don in Sweet, Brit. Fl. Gard. II, 4: *t. 403.* 1838. (T.: *Tweedie s. n. in Herb. Kew.*).

Sarcostemma Donianum Decne. loc. cit. 1844.

Sarcostemma grandiflorum (Hook.) Decne. loc. cit. 1844.

Sarcostemma incanum Decne. loc. cit. 1844. (T.: *D'Orbigny 246 in Herb. Paris*!).

Amblystigma pedunculare Benth. in Hook. Ic. Pl. 32:77. 1846. (T.: *Mandon 353 in Herb. Kew.*!).

Zosima violacea Phil. Sert. Mend. Alt. 29. 1871. (T.: *Philippi s. n.*!).

Oxystelma Gilliesii (H. & A.) K. Schum. in E. & P. Natür. Pflanzenfam. 4^2:229. 1895.

Oxystelma violacea (Phil.) K. Schum. loc. cit. 1895.

Philibertia Gilliesii H. & A. var. *pubescens* Speg. in Anal. Soc. Cient. Argent. 53:72. 1902, ex char. (T.: *Spegazzini s. n.*).
Philibertia violacea (Phil.) Schltr. in Fedde's Repert. 13:283. 1915.
Philibertia Gilliesii H. & A. var. *albida* Stuck. ex Seckt. Rev. Univ. Nac. Córdoba 17^{5-6}:70. 1930, ex char.
Philibertia Gilliesii H. & A. var. *vestita* Malme, Ark. Bot. $26A^{4}$:36. 1934, ex char.
Philibertia grandiflora Hook. f. *albida* Malme, loc. cit. 34. 1934, ex char. (T.: *Stuckert 13822 in Herb. Lillo*).
Philibertia Gilliesii H. & A. var. *grandiflora* (Hook.) T. Meyer, in Lilloa 9:452. 1943.
Philibertia Gilliesii H. & A. var. *gracilis* (D. Don) T. Meyer, loc. cit. 1943.
Philibertia Gilliesii H. & A. var. *parvicoronata* T. Meyer, loc. cit. 453. 1943. (T.: *Meyer 4117 in Herb. Lillo*!).
Philibertia Schreiteri T. Meyer, loc. cit. 436. 1943. (T.: *Schreiter 4540 in Herb. Lillo*!).
Philibertia Gilliesii H. & A. var. *mirabilis* T. Meyer, in Descole, Gen. et Sp. Pl. Argent. 2:173. 1944. (T.: *Meyer 5112 in Herb. Lillo*!).

Stems twining to rarely semi-erect, minutely puberulent in lines decurrent from the petioles; lateral branches many. Leaves narrowly lanceolate to ovate, acuminate to acute, deeply cordate, the lobes descending to converging, 2.5–4.0 cm. long, 0.3–3.2 cm. wide, membranaceous, revolute, glabrate to rather densely pilose on both surfaces, with one or more glands on the midrib at the base; petiole 1.0–2.5 cm. long. Inflorescences racemiform, 2- to 7-flowered; peduncle 1–5 cm. long, minutely puberulent; bracts linear, 0.1–0.2 cm. long; pedicels 1.0–2.5 cm. long, minutely puberulent. Calyx lobes narrowly lanceolate, 2.5 mm. long, pilosulose without, glabrous within; squamellae alternate and few, or many and indefinitely distributed within the calyx. Corolla campanulate, greenish yellow to cream with red or purple spots or streaks within, the tube 6–9 mm. long, the lobes acute to acuminate, 1.5–2.0 mm. long, glabrous to pilosulose without, glabrous within. Gynostegium 3 mm. high, the column 1 mm. long. Anthers 1.0–1.5 mm. long, the apical appendage rhomboidal, the pollinium-sacs clavate-cylindrical, 0.5 mm. long with sagittate corpusculum; ring of the corona obsolete; vesicles of the corona ovoid to subspheroid, abruptly constricted at the apex to form a more or less pronounced apiculation, abruptly constricted at their insertion upon the column, 1.5 mm. long. Ovaries 2 mm. long, glabrous; stigma-head cylindrical, 2-apiculate, the apiculae often flattened and reflexed. Follicles about 3.5 cm. long, 0.7 cm. thick; seeds unknown.

In many respects *Sarcostemma Gilliesii* is the counterpart, in subg. Oxystelma, of *Sarcostemma* (Ceramanthus) *clausum*. I have considered it to be a polytypic species which has developed a number of races, apparently in response largely to increasing aridity. These populations, however, do not appear to be sufficiently distinct to be classified even as subspecies and therefore are not recognized nomenclaturally. The element known as *Philibertia gracilis* is, for the most part, northern (Bolivia and adjacent Argentina), and is a slender vine with broad, cordate, membranaceous, and glabrous leaves. In the southern provinces of Argentina is the so-called variety *pubescens* of *P. Gilliesii*, with narrow, hastate, subcoriaceous, and densely pubescent leaves. More or less intermediate geographically and morphologically (but broadly overlapping at both extremes) is the typical *S. Gilliesii*.

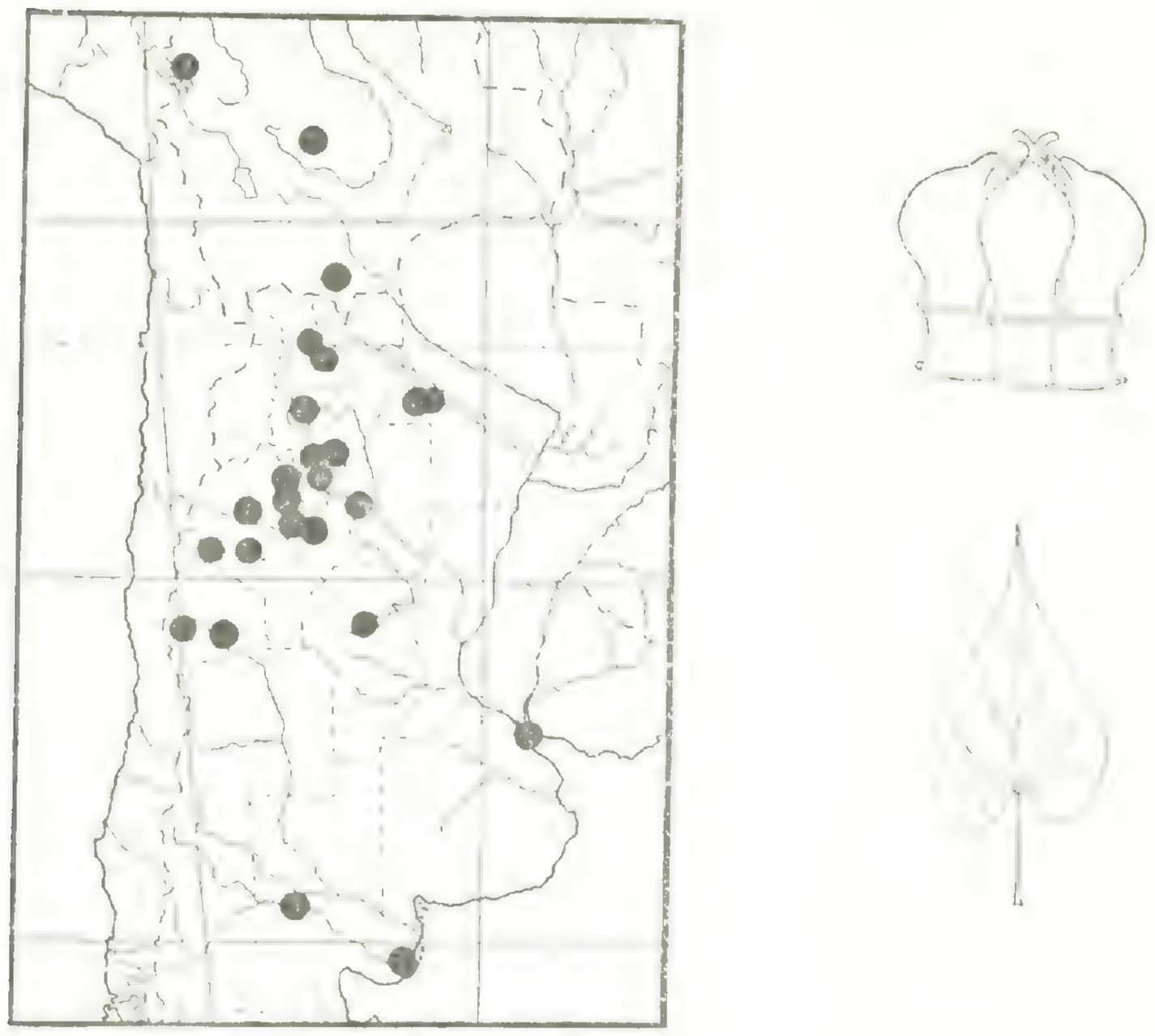

Fig. 19. Distribution, gynostegium, and leaf of S. *Gilliesii*.

There are also several local variants which are of interest: var. *parvicoronata* of T. Meyer includes those relatively common, but by no means distinct, forms in which the corona vesicles are shrunken and linear in outline; *P. Schreiteri* Meyer is a form with follicles of such a degree of rugosity that they appear squamate; *P. grandiflora* Hook. has larger flowers and lanceolate leaves rather more pubescent beneath than above. Except for the characters mentioned, these variants possess all of the attributes of *Sarcostemma Gilliesii*. Whether they are to be recognized as varieties is a matter of preference which should, however, be based upon experience with the genus as a whole. I prefer not to do so until population studies can be made. I can find no altitudinal, habitat, or flowering period differences among the various subgroups of S. *Gilliesii*, except for the obvious fact that those from the more southern stations experience greater aridity.

Sarcostemma Gilliesii is a sub-shrub of twining to trailing habit. Like other desert species of the genus, it makes tangled masses several feet in diameter, climbing over rocks and shrubs, as well as itself, in dry, rocky soil. Occasionally it may climb into trees. It grows at altitudes from 450 to 3000 feet and has been collected in flower from September to March. I have seen no fruit, except for a single distorted follicle collected in August. An interesting specimen was collected among ballast at Karghus Point, New Jersey. According to the collector, Dr. Henry Leffmann, in a letter to Asa Gray, it was a perennial which flowered abundantly but did not fruit.

BRAZIL (?): Río Negro, *D'Orbigny 246*, type of S. *incanum* Decne.
BOLIVIA. COCHABAMBA: quebradas de Totara, *Steinbach 5992;* near Yungas, *Rusby 1973*. LA PAZ: near Sorata, *Mandon 353*, type of *Amblystigma pedunculare* Benth. TARIJA: near Tarija, *Fiebrig 2668*.
ARGENTINA. BUENOS AIRES: Monte Hermoso, *Carette s. n.;* island near Buenos Aires, *Tweedie s. n.;* Isla Martín García, *Cabrera 2846*. CATAMARCA: Capitál, Alta Chaya, *Castillón 1071;* El Cajon, Las Visacheras, *Castillón 3349;* Pomán, near Pomán, *Castillón 1029* (part); Ambato, El Potrero, *Castillón 1069;* Capitál, *Castillón 1072, 1958;* Valle de Santa Maria, Punto de Balasto, *Schreiter s. n.;* Andalgalá, Andalgalá, *Jörgensen 1095;* Tinogasta, Vallecito a Agua Negro, *Schreiter 6284;* Ambato, El Rodeo, *Castillón s. n.* CHACO: Nueva Pompeya, *Jörgensen 3025*. CÓRDOBA: Córdoba, Río II, *Stuckert 23264;* Malagueño, *Bartlett 20069;* near La Falda, *Job 515; Kuntze s. n., Stuckert s. n., Lössen 39*. FORMOSA: Guayculec, *Jörgensen 3184*. JUJUY: Tilcara, Cerro Péna, *Venturi 4939;* Tilcara, Maimara, Hualchin, *Budin s. n.;* Humahuaca, quebrada de Humahuaca, El Volcán, *Castillón 6421;* Volcán, Loma de Laguna, *Schreiter 2590;* Tilcara, quebrada de Euasamayo, *E. K. Balls B5962*. LA RIOJA: Famatina, Famatina, *T. Meyer 4255;* Generál Lavalle, Guandacol, *T. Meyer 4182*. MENDOZA: Pampa de St. Rafael, *Wilczeb 281;* Maipu, Barrancas, *Bartlett 19335;* Potrerillos, *Bartlett 19325;* between Villavicencia and Uspullata, *Senn 4452*. RÍO NEGRO: vicinity of Generál Roca, *Fischer 110*. SALTA: San José, *Lorentz & Hieronymus 221;* Capitál, Salta, *Hunziker 2722*. SANTIAGO DEL ESTERO: Gramilla, *Venturi 10281*. TUCUMÁN: Trancas, Tapia, *Schreiter 3495;* Río Chico, La Cocha, *Bailetti 148, 350, 545;* Trancas, Raco, *Venturi 1202;* Trancas, Chaspiyacu, *Schreiter 5514;* Capitál, *Lillo 320, 11864;* Tafí, Amaicha, *Castillón 2485, Schreiter 5511;* Trancas, Tapia, *Venturi 1114, Lillo 4840, Rodriguez 596;* Trancas, Vipos, *Venturi 1717, Schreiter 4540*, type of *P. Schreiteri* Meyer; Burruyacu, Cerro del Campo, *Venturi 7720;* Capitál, Villa Luian, *Venturi 280;* Capitál, Barranca Colorada, *Venturi 4095;* Tafí, La Casita, region del Aliso, *Lillo 7350;* Burruyacu, Cerro de Durasnillo, *Monetti 1992;* Tucumán, *Tweedie s. n.*, type of *P. grandiflorum* Hook.

17. SARCOSTEMMA **Vaileae** (Rusby) R. Holm, comb. nov.

Oxystelma Vaileae Rusby, in Bull. N. Y. Bot. Gard. 4:315. 1907. (T.: *Bang 985 in Herb. N. Y. Bot. Gard.*!).
Philibertia albiflora Lillo, in Physis 4:428. 1919. (T.: *Castillón 9463 in Herb. Lillo!*).

Stems twining, minutely pilosulose in lines decurrent from the petioles; lateral branches many. Leaves deltoid-lanceolate, acute to obtuse, shallowly cordate, the lobes descending or diverging, 2.9–7.0 cm. long, 0.8–2.9 cm. wide, glabrate to minutely pilosulose above, glabrate to subtomentose beneath, with one or more glands on the midrib at the base; petiole 1.9–2.9 cm. long. Inflorescences racemiform, 2- to 7-flowered; peduncle 1–5 cm. long, minutely pilosulose; bracts linear, 0.1–0.2 cm. long; pedicels 1.0–2.5 cm. long, minutely pilosulose. Calyx lobes narrowly lanceolate, 3 mm. long, pilosulose without, scatteringly pilosulose within; squamellae numerous, indefinitely distributed within the calyx. Corolla campanulate, yellowish green to cream-colored, the tube 6 mm. long, the lobes acute, 2.5–3.0 mm. long, pilosulose without, glabrous within. Gynostegium 3 mm. high, the column 0.75 mm. long. Anthers 1.5 mm. long, the apical appendage rhomboidal, the pollinium-sacs clavate-oblongoid, 0.5 mm. long, with sagittate corpusculum; ring of the corona nearly obsolete; vesicles of the corona obovoid-oblongoid, with a short apical appendage, rarely with a vertical ventral keel, constricted at their insertion upon the column, 1.5 mm. long. Ovaries 2 mm. long, glabrous; stigma-head cylindrical, shortly 2-fid. Follicles and seeds unknown.

Sarcostemma Vaileae is most closely related to *S. Gilliesii*. It may perhaps represent a race of that variable species which has become stabilized and no longer intergrades to an appreciable extent. Although the species are rather close morphologically, there is little difficulty in distinguishing them, for they differ not only in many vegetative characters but in several aspects of the flower as well. A general scarcity of pigmentation gives the stem, leaves, and flowers a characteristic pallid aspect. The column and anthers, on the other hand, are unusually dark, or even black, contrasting strongly with the white or yellow corona vesicles and corolla.

The collection, *Fiebrig 3084*, is the type of *Philibertia picta* Schltr. and is a form with dark flowers and light column. It is possibly a hybrid between *S. Vaileae* and *S. Gilliesii*, for the vegetative characters are those of the former species, but I prefer not to place the name in synonymy of either of these species at present. There are several collections, e. g. *Steinbach 8726*, which superficially match the type of *P. picta*, but which actually are easily referable to *S. solanoides* on the basis of the pubescence of the leaves, the character of the gynostegium, and the inflorescence.

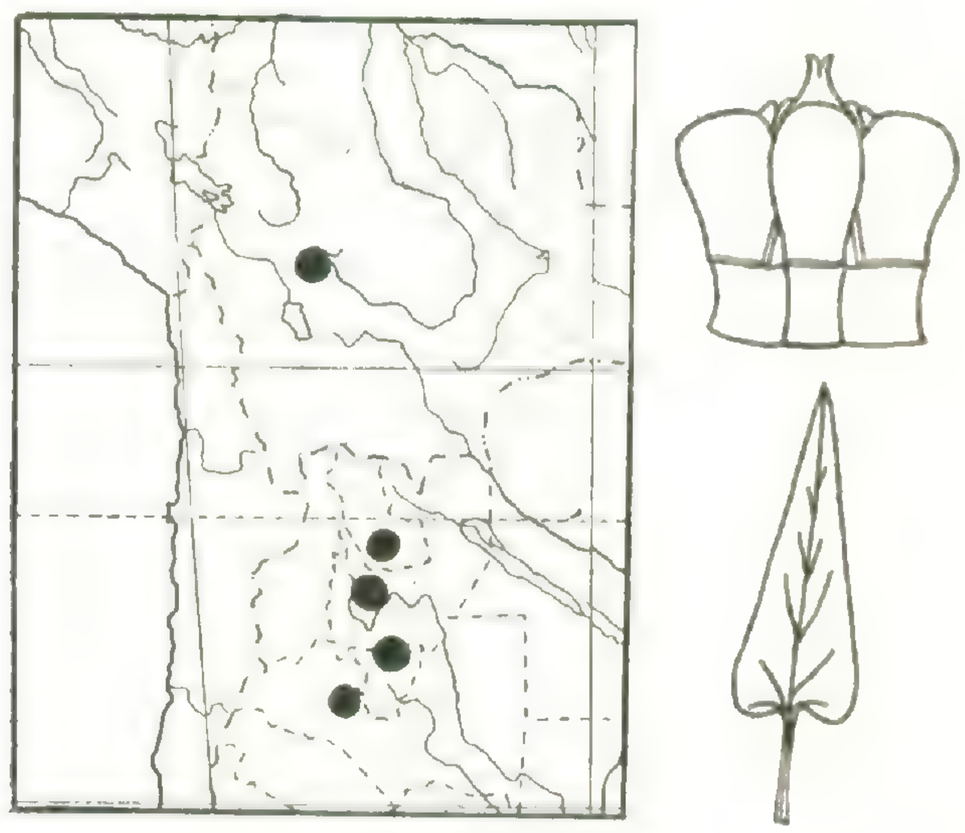

Fig. 20. Distribution, gynostegium, and leaf of *S. Vaileae*.

Sarcostemma Vaileae has been collected in Bolivia and northern Argentina in open woods at altitudes from 3500 feet to 6000 feet. Flowering specimens are dated December to March.

BOLIVIA. COCHABAMBA: Cochabamba, *Bang 985*, type of *Oxystelma Vaileae* Rusby. ARGENTINA. CATAMARCA: Andalgalá, El Candado, *Jörgensen 1239*; Belén, Villavil, *Schreiter 10255*. JUJUY: Tumbaya, El Volcán, *Castillón 6473*. SALTA: Rosario de Lerma, Campo Quijano, *Venturi 8064*; Cerro San Bernardo, *West 6130*. TUCUMÁN: Trancas, San Pedro de Colalao, *Castillón 6781*.

18. SARCOSTEMMA SOLANOIDES (HBK.) Decne. in DC. Prodr. 8:541. 1844.

Philibertia solanoides HBK. Nov. Gen. et Sp. Pl. 3:196, *t. 230*. 1819. (T.: *Humboldt & Bonpland s. n. in Herb. Paris*!).
Philibertia flava Meyen, Reise 1:466. 1834, ex char.
Pentagonium flavum (Meyen) Schauer in Nova Acta Acad. Caes. Leop. Nat. Cur. 19. Suppl. 1:364. 1843.

Sarcostemma hastatum Decne. loc. cit. 1844. (T.: *Dombey s. n. in Herb. Paris!*).
Sarcostemma marsupiflorum Decne. loc. cit. 1844. (T.: *Cuming 983 in Herb. Kew.*!).
Sarcostemma quadriflorum Decne. loc. cit. 542. 1844. (T.: *Matthews 576 in Herb. Delessert*!).
Sarcostemma variifolium Decne. loc. cit. 1844. (T.: *Dombey s. n. in Herb. Paris*!).
Oxystelma solanoides (HBK.) K. Schum. in E. & P. Natür. Pflanzenfam. 4^2:229. 1895.
Philibertia Weberbaueri Schltr. in Engl. Bot. Jahrb. 37:607. 1906. (T.: *Weberbauer 2742 in Herb. Berol.*!).
Philibertia quadriflora (Decne.) Schltr. in Fedde's Repert. 13:282. 1915.
Philibertia variifolia (Decne.) Schltr. loc. cit. 283. 1915.
Philibertia obtusiuscula Malme, in Ark. Bot. $25A^7$:16, *fig. 2*. 1933. (T.: *Hicken 39 in Herb. Stockholm*!).
Philibertia obtusata Malme, op. cit. $26A^4$:41. 1934, *sphalm.*

Stems twining or trailing, minutely puberulent; lateral branches many. Leaves ovate to deltoid-lanceolate, acute to acuminate, deeply cordate, the lobes diverging, 2.0–3.5 cm. long, 0.9–1.4 cm. wide, membranaceous to subcoriaceous, often somewhat undulate, scatteringly puberulent above, subtomentose beneath, with one or more glands on the midrib at the base; petiole 0.6–0.9 cm. long. Inflorescences umbelliform, 4- to 10-flowered; peduncle stout, slightly recurved at the apex, 3.5–7.5 cm. long, minutely puberulent; bracts linear, 0.1–0.2 cm. long; pedicels 0.9–1.3 cm. long, minutely puberulent. Calyx lobes narrowly lanceolate, 3–5 mm. long, scatteringly to densely puberulent without, glabrous within; squamellae absent, single, or paired. Corolla rotate-subcampanulate, greenish-yellow to cream with red or purple spots within, or uniformly greenish-yellow, the tube 5–6 mm. long, the lobes acute, 3–4 mm. long, puberulent without, glabrous within. Gynostegium 2–3 mm. high, vernicose, the column about 1 mm. long. Anthers 1.0–1.5 mm. long, the apical appendage deltoid, the pollinium-sacs compressed, obclavate, 0.5 mm. long, with sagittate corpusculum; ring of the corona short; vesicles of the corona truncate-oblongoid, with or without a small apiculation at the apex, 1.5 mm. long. Ovaries 2 mm. long, glabrous; stigma-head cylindrical, obscurely depressed or 2-lobed apically. Follicles ovoid, minutely puberulent, finely striate, 4.4 cm. long, 0.8 cm. thick; seeds unknown.

The umbelliform inflorescence and rotate-subcampanulate flowers at once distinguish this species from others of the subg. OXYSTELMA. Superficially, in fact, S. *solanoides* appears to pertain rather to the subg. CERAMANTHUS. This resemblance is most probably due to convergence, however, for not only the structure of the gynostegium, but also the detailed morphology of the inflorescences and vegetative organs relates it clearly to OXYSTELMA. The corona ring is very abbreviated and free from the corolla only at the outermost part, and the gynostegium is vernicose. The inflorescence, while umbelliform, is slightly recurved at the apex, a condition which does not obtain in subg. CERAMANTHUS.

Sarcostemma solanoides apparently is a trailing plant forming dense mats (but not rooting at the nodes), in dry, rocky, or gravelly soil or on talus slopes. In more favorable habitats it climbs into shrubs. It is reported that the herbage has an onion-like odor when crushed, presumably like that of S. *hirtellum*. The species

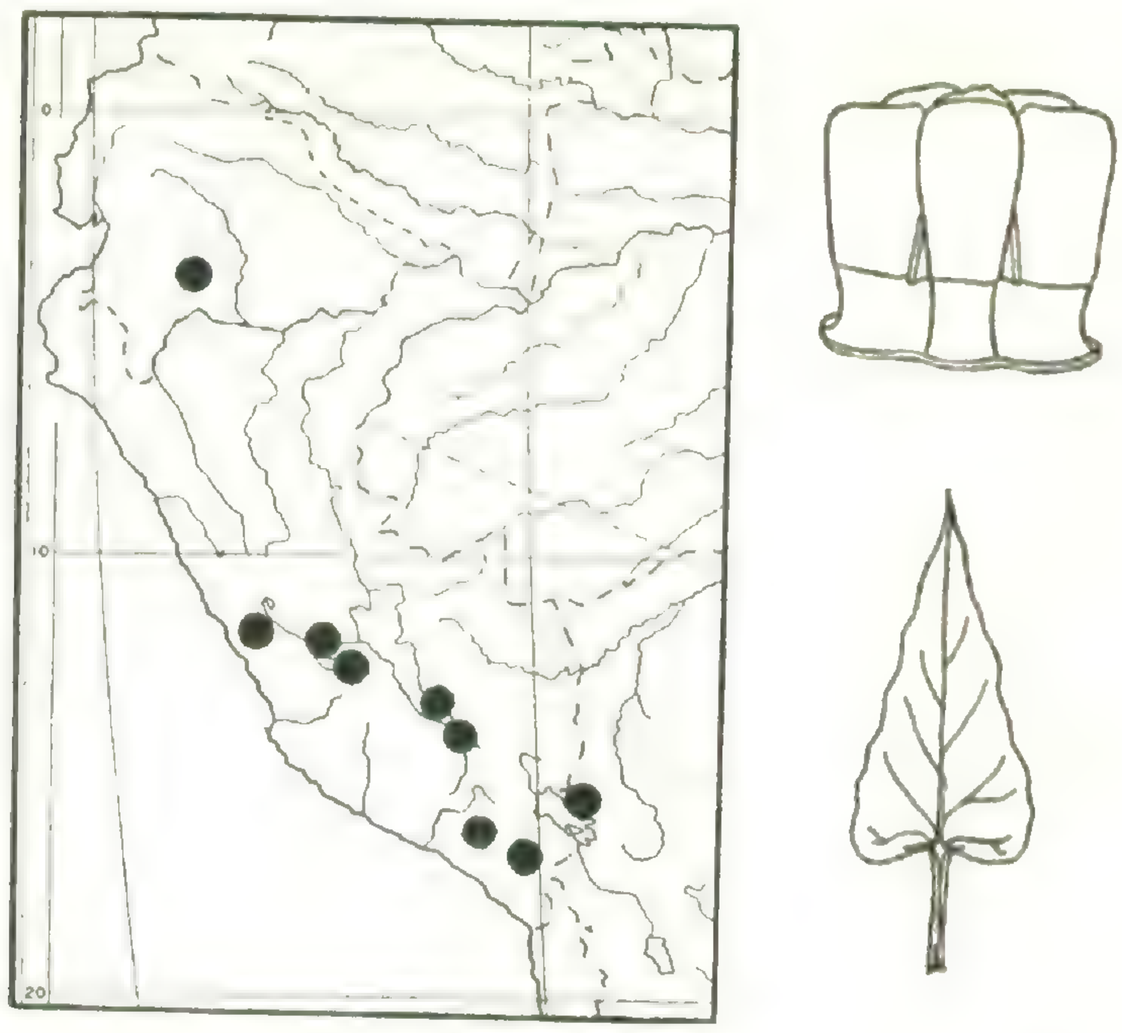

Fig. 21. Distribution, gynostegium, and leaf of *S. solanoides*.

ranges from southern Ecuador to northern Bolivia and has been collected in flower from February to April at altitudes from 6500 to 15000 feet.

ECUADOR. LOJA: between San Pedro & Chinchas, ca. 55 km. from Loja, *Espinosa 1291*; Hac. Huaico-Pamba, ca. 55 km. S Loja, *Espinosa 2303*.

PERU. AREQUIPA: Arequipa, *Pennell 13195*. CUZCO: Paruro, Huanoquite, *Vargas 2347*; Cuzco, Callchaca, *Vargas 5507*; Canchis, slopes of Sicuani, *Vargas 9829*, *Stafford 359*; Sicuano, *Hicken 39*, type of *P. obtusiuscula* Malme. LIMA: Huarochiri, valley of Río Rimac, 81 km. E of Lima, *Goodspeed & Metcalf 30229*; Huarochiri Matucana, *Weberbauer 5257*, *Macbride 2889*, *Macbride & Featherstone 208*; Orroya near Lima, *Kalenborn 30*. HUANCAVELICA: Angaraes, 3 km. W of Huanta, *Stork & Horton 10809*; Tayacaja, Montaro Valley near La Mjorada, *Weberbauer 7610*; Tayacaja, Montaro Valley below Colabamba, *Weberbauer 6453*. LIMA: Río Blanco, *Macbride 3042*. MOQUEGUA: Carumas, *Weberbauer 7298*.

BOLIVIA. COCHABAMBA: Tal von Sacaba, *Steinbach 8726*. LA PAZ: near Sorata, *Mandon 360*.

19. SARCOSTEMMA **stipitatum** (Lillo) R. Holm, comb. nov.

Philibertia stipitata Lillo, in Physis 4:429. 1919. (T.: *Lillo 2621 in Herb. Lil!o!*).

Stems twining, glabrous or minutely pilosulose in lines decurrent from the petioles; lateral branches relatively few. Leaves lanceolate, acuminate, cordate, the lobes descending, 5.5–7.5 cm. long, 1.5–3.0 cm. wide, firmly membranaceous, undulate-crispate, essentially glabrous on both surfaces, the veins pilosulose, with one or more glands on the midrib at the base; petiole 1.0–2.5 cm. long. Inflorescences racemiform, 4- to 8-flowered; peduncle 3.0–5.8 cm. long, minutely appressed-pilosulose; bracts linear, 0.2–0.3 cm. long; pedicels 0.7–1.1 cm. long, minutely pilosulose. Calyx lobes narrowly lanceolate, 3.5 mm. long, appressed-pilosulose on both surfaces; squamellae few or absent, alternate. Corolla urceolate-campanulate, the tube 6 mm. long, the lobes bright brown, obtuse, 3 mm. long,

puberulent without, glabrous within. Gynostegium 3.5 mm. high, the column 1.5 mm. long. Anthers 1.5 mm. long, the apical appendage ovoid, slightly emarginate, the pollinium-sacs clavate-oblongoid, somewhat flattened, with a sterile hyaline region at the attachment of the translator arm, 0.75 mm. long, with narrowly ellipsoid corpusculum; ring of the corona nearly obsolete; vesicles of the corona oblate-spheroid, 1 mm. long. Ovaries 2 mm. long, glabrous, the styles well-marked; stigma-head cylindrical, obscurely depressed apically. Follicles and seeds unknown.

Sarcostemma stipitatum surely is the most distinctive species of the subg. OXYSTELMA, with its urceolate corolla, greatly reduced corona vesicles, and pollinia with a sterile, hyaline region, yet, surprisingly enough, it has never been referred to another genus. It is without obvious relationship to any other species to my knowledge. Rather sharply localized in northern Argentina, it grows at altitudes from 4500 to 5500 feet, and flowers from November to January.

ARGENTINA. SALTA: La Candelaria, Cuesta del Unquillo, *Schreiter 9372*. TUCUMÁN: Tafí, La Hoyada, *Venturi 1536;* Quebrada del Durasnillo, *Lillo 2621*, *Schreiter 8703;* Tafí, Cumbre del Siambón, *Venturi 2821*.

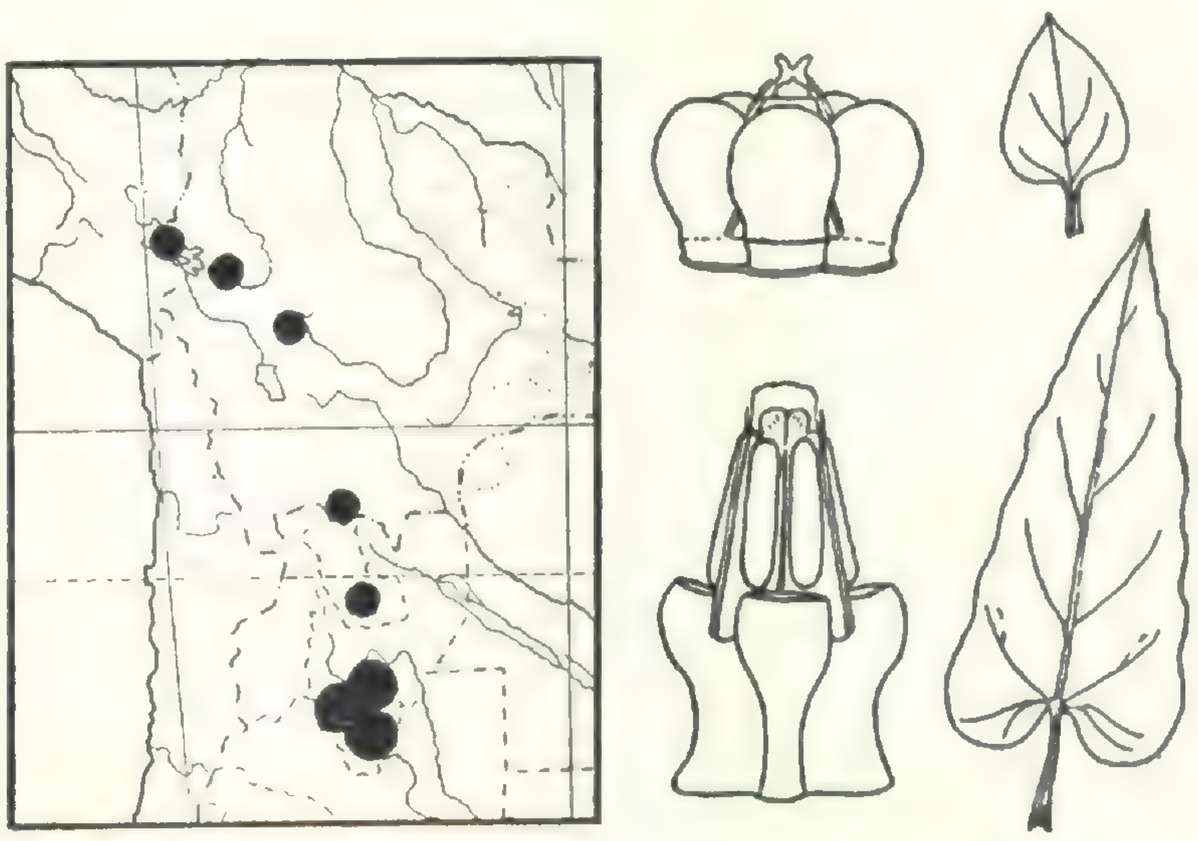

Fig. 22. Distribution of *S. stipitatum* (small dots), of *S. lysimachioides* (large dots). Gynostegium and leaf of *S. lysimachioides* (upper figures), of *S. stipitatum* (lower figures).

20. SARCOSTEMMA **lysimachioides** (Wedd.) R. Holm, comb. nov.

Lugonia lysimachioides Wedd. Chlor. And. 2:49, *t. 54*. 1857. (T.: *Weddell 4136 in Herb. Paris*!).
Philibertia lysimachioides (Wedd.) T. Meyer in Descole, Gen. et Sp. Pl. Arg. 2:177. 1944.

Stems prostrate, trailing from a short woody caudex, more or less articulate, minutely appressed-pilosulose; lateral branches many on the old stems. Leaves ovate, acute to obtuse, usually cordate, sometimes truncate or obtuse, 0.4–1.0 cm. long, 0.3–0.6 cm. wide, subcoriaceous, revolute, essentially glabrous on both sur-

faces, the midrib puberulous, usually without glands at the base (rarely a very few); petiole 0.2–0.4 cm. long. Inflorescences racemiform, 1- to 3-flowered; peduncle 0.4–0.7 cm. long, minutely pilosulose; bracts linear, 0.1–0.2 cm. long; pedicels 0.3–1.0 cm. long, appressed-pilosulose. Calyx lobes lanceolate to oblanceolate, 4 mm. long, puberulent without, glabrous within; squamellae alternate, 3–5, upon a thickened pad. Corolla campanulate, the tube 5.5 mm. long, the lobes deep orange to red, ovate, broadly obtuse, 5.5–6.0 mm. long, scatteringly puberulent without, glabrous within. Gynostegium 3 mm. high, the column 0.5 mm. long. Anthers 1.5 mm. long, the apical appendage deltoid, the pollinium-sacs clavate, 0.5 mm. long, with sagittate corpusculum; ring of the corona obsolete; vesicles of the corona ovoid, slightly constricted at their insertion upon the column, 1 mm. long. Ovaries 2 mm. long, glabrous, the styles well-marked; stigma-head conical, 2-apiculate, the apiculae flattened. Follicles fusiform, 1.9 cm. long, 0.3 cm. thick, minutely puberulent, finely striate; seeds unequally biconvex, 3 mm. long, 1.5 mm. wide, rugose on both surfaces, the margin entire; coma about 0.8 cm. long.

A plant of pronounced alpine modification, S. *lysimachioides* grows at heights of 9000 to 14000 feet in the Andes of Peru, Bolivia, and Argentina. It is a prostrate, perennial herb forming clumps among bunch grasses and shrubs. To precisely which species of *Sarcostemma* it is most closely related I am unable to determine. The corolla and gynostegium are reminiscent of S. *solanoides*, but the fact that the corolla is adnate to the column forms a clear distinction. This condition otherwise is found only in S. *andinum*, yet despite the fact that the latter and S. *lysimachioides* were included in the same segregate genus *(Lugonia)* in the past, I feel that they are only distantly related. *Sarcostemma lysimachioides* has been found in flower from November to February, and in fruit in April.

PERU. PUNO: Baja Isla del Lago Titicaca, *Mexia 7789;* Granja Salcedo, Cañon of Viscachani, *Mexia 04261.*

BOLIVIA. AYOPAYA: *Weddell 4136,* type of *L. lysimachioides* Wedd. CHUQUISACA: Tomina, *Weddell s. n., 3885;* Cinti, *Weddell 3938.* COCHABAMBA: Cochabamba, *Weddell 4102;* Ansaldo, *Cárdenas 2292.* LA PAZ: La Paz, *Buchtien 67;* Omasuyos, *Mandon 359.* TARIJA: about 45 km. NE of Villazón on Villa Montes, *West 8234;* Escayache bei Tarija, *Fiebrig 3033.*

ARGENTINA. JUJUY: Tumbaya, Mula Muerta, *Castillón 6665.*

Section 2. PENTACYPHUS (Schltr.) R. Holm, stat. nov.

Pentacyphus Schltr. in Engl. Bot. Jahrb. 37:605, *fig. 3.* 1906, as genus.

This section includes two species in which the corolla tube is adnate to the column and pubescent within, forming five hairy pouches alternating with the stamens. The column has deep grooves, and the large flowers have broadly obtuse corolla lobes.

KEY TO THE SPECIES

a. Leaves oblong-lanceolate, cordate; inflorescences racemiform, 2-flowered; corona segments undivided, depressed dorsally ..... 21. *S. andinum*

aa. Leaves obovate-elliptic, cuneate; inflorescences umbelliform, several-flowered; corona segments bipartite ..... 22. *S. Lehmannii*

21. SARCOSTEMMA andinum (Ball) R. Holm, comb. nov.

Lugonia andina Ball, in Jour. Linn. Soc. Lond. 22:49. 1887. (T.: *Ball s. n. in Herb. Kew.*!).

Pentacyphus boliviensis Schltr. in Engl. Bot. Jahrb. 37:605, *fig. 3*. 1906, ex char. (T.: *Weberbauer 179 in Herb. Berol.*).

Stems twining, glabrous or pilosulose in lines decurrent from the petioles; lateral branches many. Leaves oblong-lanceolate, acute to mucronate, cordate, the lobes descending, 1.5–5.0 cm. long, 0.6–2.4 cm. wide, membranaceous, glabrous above, the veins pilosulose, with one or more glands on the midrib at the base, appressed-pilosulose beneath; petiole 0.6–2.5 cm. long. Inflorescences racemiform, consisting of two 1-flowered cymules; peduncle 1–2 cm. long, minutely pilosulose; bracts linear, minute; pedicels 0.5–1.5 cm. long, minutely puberulent. Calyx lobes narrowly lanceolate, 8 mm. long, sparsely puberulent without, glabrous within, ciliolate; squamellae absent. Corolla campanulate, green to yellow, the lobes with a purple to dark red spot at the base, the tube 9.5 mm. long, glabrous without, pilosulose within, adnate to the column directly below the anthers forming five hairy pouches, each with a tuft of longer hairs borne upon a thickened pad at the base, the lobes broadly ovate, obtuse, 9 mm. long, glabrous on both surfaces. Gynostegium 7 mm. high, the column 4 mm. long, grooved between the stamens with the margins of the groove produced and arrect. Anthers 1.5 mm. long, the apical appendage oblong, mucronate, the pollinium-sacs oblongoid, somewhat flattened, 0.75 mm. long, with ellipsoid-sagittate corpusculum; ring of the corona obsolete; vesicles of the corona obovoid, depressed dorsally toward the apex, attenuate, 3 mm. long. Ovaries 4 mm. long, glabrous, the styles not well-marked; stigma-head 2-lobed. Follicles and seeds unknown.

Sarcostemma andinum has diverged markedly in a number of ways from the general OXYSTELMA type. The corolla is adnate to the column along five lines directly below the anthers; below the point of attachment the corolla tube is pilosulose within, so that five hairy pouches are formed. Exterior to these, the corolla is quite glabrous. The highly vernicose gynostegium is similarly extreme: as in several species of the subg. CERAMANTHUS, the column is grooved or invaginated directly below the anther wings, but in this case, the margins of the groove are produced at an angle of about 45° to the column. Continuous with the anther wings they, in effect, extend the latter the length of the column, down into the pouches, to the base of the corolla. Such modifications surely must adapt the flower very specifically to its insect pollinator.

These distinctive features of the plant, together with others of the inflorescence and pollinia, preclude relating S. *andinum* to any other species in the family except S. *Lehmannii*. The latter species is so distinct that it also has been considered, with

a certain justification, as a representative of a monotypic genus. I see no advantage in maintaining monotypic genera for such plants, however. To include them within another genus, separating them from the other species with appropriate subgeneric categories, at least indicates their affinities in a general way. Isolating them in a family with no adequate system of tribes conveys nothing as to their relationships, morphological or otherwise, and makes identification immeasurably more difficult.

Sarcostemma andinum is a widespreading vine, which grows in shady or open situations, climbing over shrubs and trees. It has been collected at altitudes from 5500 to 13000 feet; flowering specimens are dated from February to June.

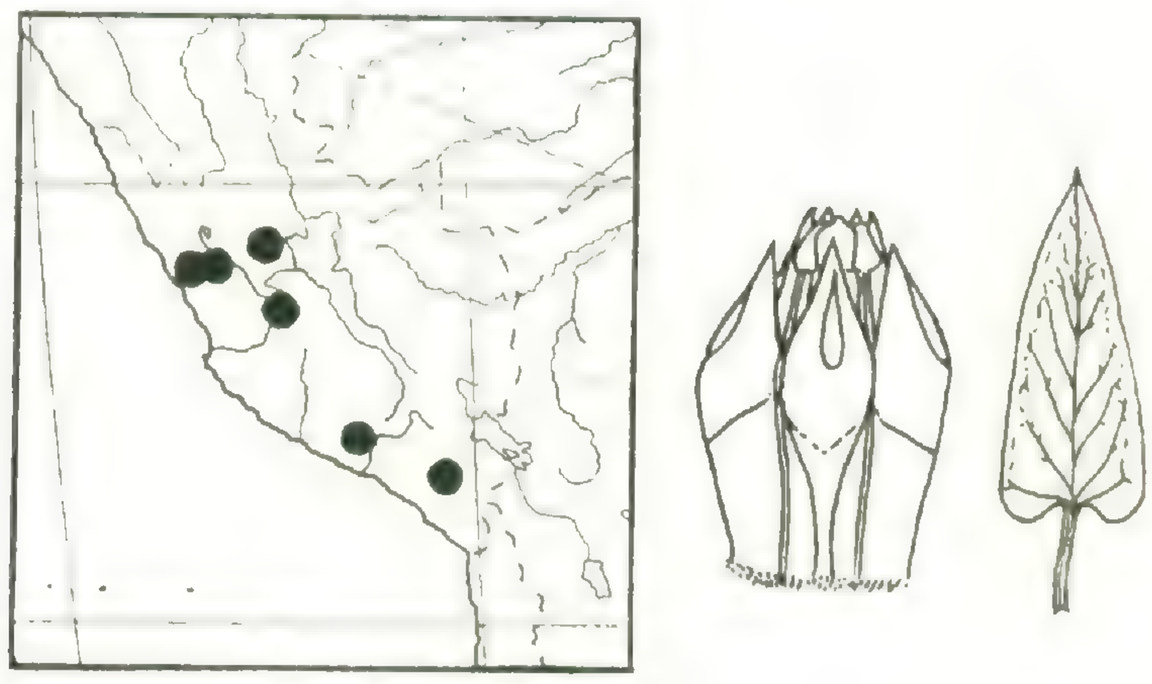

Fig. 23. Distribution, gynostegium, and leaf of *S. andinum*.

PERU. AREQUIPA: *Weberbauer 6860.* HUANCAVELICA: Castrovirreina, near Córdoba, *Metcalf 30274.* LIMA: Huarochiri, valley of Río Rimac, 50 km. E of Lima, *Goodspeed 33090;* Huarochiri, Infiernillo, *Goodspeed, Stork & Horton 11602;* Huaros, *Pennell 14722;* Río Blanco, *Killip & Smith 21701, Macbride & Featherstone 725;* Matucana, *Macbride 2951;* near Lima, *Kalenborn 30;* Chicla, *J. Ball s. n.,* type of *L. andina* Ball. MOQUEGUA: Carumas, *Weberbauer 7258.*

22. SARCOSTEMMA **Lehmannii** (Schltr.) R. Holm, comb. nov.

Tetraphysa Lehmannii Schltr. in Engl. Bot. Jahrb. 37:616. 1906, ex char. (T.: *Lehmann 8516 in Herb. Berol.*).

Stems twining, more or less articulate, glabrous; lateral branches few. Leaves obovate-elliptic, acute, cuneate, 9.5 cm. long, 4.0 cm. wide, coriaceous, glabrate, with several glands on the midrib at the base; petiole 1.5 cm. long. Inflorescences umbelliform, several-flowered; peduncle 2 cm. long, glabrous; bracts linear-lanceolate, 0.3–0.4 cm. long; pedicels 2.5 cm. long, glabrous. Calyx lobes obovate-elliptic, 7 mm. long, glabrous on both surfaces; squamellae alternate, solitary. Corolla campanulate, cream with reddish-purple spots within, the tube 7 mm. long, glabrous without, pilosulose within, adnate to the column directly below the anthers forming five hairy pouches, the lobes broadly ovate, obtuse, 15 mm. long, glabrous without, glabrous to minutely pilosulose within. Gynostegium 7 mm. high, the column 4 mm. long, grooved between the stamens (with the margins of

the groove slightly produced) and directly below the corona vesicles. Anthers 1.5 mm. long, the apical appendage oblong, the pollinium-sacs oblongoid, somewhat flattened, 0.5 mm. long, with ellipsoid corpusculum; ring of the corona obsolete; vesicles of the corona bipartite, consisting of two somewhat flattened, ovate, attenuate segments, joined toward the apex, exceeding the stigma-head in length. Ovaries 3 mm. long, glabrous, the styles not well-marked; stigma-head 2-lobed. Follicles and seeds unknown.

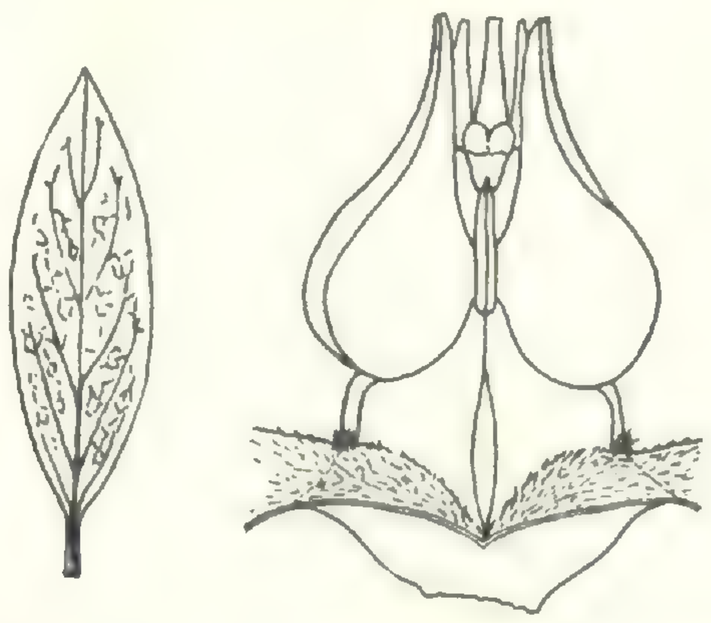

Fig. 24. Leaf and gynostegium of S. *Lehmannii*.

A most rare and distinctive species. I have not seen the type, but the description and figures of Schlechter leave no doubt as to its identity with the single subsequent collection available to me. The gynostegium is highly vernicose and superficially similar to that of *Sarcostemma andinum*. In addition to the five grooves in the column which lead into the pouches of the corolla tube, there are five longitudinal clefts which divide the corona vesicles, and the column directly below them, to the corolla. As I have indicated in the discussion of the preceding species, S. *Lehmannii* is probably most closely related to S. *andinum*. The evolution of the gynostegium may be pictured as involving an extension of the dorsal depression of the corona vesicles of the latter species, until it extends to the corolla. The advantages of such an arrangement to the plant are not in the least apparent, however. If these forms are to be related to any group in the Asclepiadaceae, it must surely be to *Sarcostemma*. I have merged them with that genus, indicating their divergence by sectional segregation, rather than let them drift among the many other monotypic genera without obvious mooring.

Sarcostemma Lehmannii has been collected in dense woods at altitudes of about 8000 feet, and was in flower in May and October.

COLOMBIA. CAUCA: vicinity of Popayan, *Lehmann 8516*, type of *T. Lehmannii* Schltr., not seen.

ECUADOR. LOJA: between Tambo Cachiyacu, La Entrada, and Nudo de Sabanillas, *Steyermark 54471*.

IMPERFECTLY KNOWN SPECIES

Sarcostemma Jacquini Decne. in DC. Prodr. 8:542. 1844. Description inadequate, no type cited.

Sarcostemma trichopetalum Alv. Silv., Fl. Serr. Mineir. 18. 1908. Publication unavailable to me.

EXCLUDED SPECIES

Philibertia anomala T. S. Brandeg. in Univ. Calif. Publ. Bot. 4:277. 1912. = BLEPHARODON MUCRONATUM (Schlecht.) Decne.

Lugonia micrantha Malme, in Nova Acta Acad. Soc. Upsal. IV, 1[1]:115. 1905. = APHANOSTELMA MICRANTHUM (Malme) T. Meyer.

Philibertia ? scandens Gomez, in Anal. Hist. Nat. Madrid 23:276. 1894. = FISCHERIA SCANDENS DC.

Philibertia viridiflora (Torr.) Britt. & Rusby, in Trans. N. Y. Acad. Sci. 7:11. 1887, sphalm.

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Italicized numbers refer to the collectors' numbers, *s. n. (sine numero)* to unnumbered collections; parenthetical numerals indicate the numbers of the taxonomic entities recognized in this monograph. Only specimens from the Western Hemisphere are included.

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THE GRAIN AMARANTHS: A SURVEY OF THEIR HISTORY AND CLASSIFICATION*

JONATHAN DEININGER SAUER**

Since man first began digging, clearing, and burning the natural vegetative mantle of the earth, certain plant groups have multiplied and spread as others declined and retreated; they have thrived in the midst of the general destruction as weedy followers or cultivated allies of civilization. In the great story of how such plants and human civilizations have consorted, migrated, and evolved together on the earth, the amaranths have played a part which is of uncommon ethnological and botanical interest.

For the ethnologist, the amaranths present problems of curiously widespread and ancient culture traits. The plants are firmly entrenched in the religious and economic lives of various Old and New World peoples as wild or cultivated grains, pot-herbs, dye-plants, fetishes, and ornamentals. Insight into their culture history should help in understanding the larger problem of the origin and diffusion of cultivated plants.

For the botanist, the amaranths present a problem of strikingly contrasting responses to man by different members of a single genus. Some species have remained aloof as unobtrusive wild endemics. Others have moved uninvited into clearings and fields; with the unintentional help of man they have become aggressive and widespread weeds. Still others have entered cultivation and become deliberately propagated wards of man. Insight into the unlike behavior of these different amaranths should help in understanding the larger problem of changes in character and distribution patterns of plants since the coming of man.

In spite of its uncommon interest, the story of the amaranths has remained neglected and obscure. Perhaps this is partly because the problem cannot be readily attacked either by a strictly ethnological or by a strictly taxonomic approach. The ethnologist is confronted by near chaos in the classification and nomenclature of this group; he can make little headway until there is clearer definition of the botanical entities which have entered into culture history. The taxonomist is confronted by a dim and fragmentary picture of the relationships of man to this group; he can make little headway until there is clearer recognition of the effects of artificial processes in the evolution and distribution of the botanical entities. A combined ethnological and botanical investigation would seem to be the only way to escape from the dilemma.

In this paper these two complementary lines of approach will be tried on a limited sector of the general problem. The full story of all the wild, weed, and cultivated species of this genus is much too massive a problem to be attacked here. This paper will focus on the cultivated grain amaranths; even within this restricted

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* An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Washington University.

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group, it can make no more than a beginning.

The grain amaranths are an attractive starting point for several reasons. Of all the amaranths, the grain species seem to have been most closely and most anciently allied with man; they have left the deepest imprint on human cultures and received in return the clearest marks of human selection and dispersal. A fund of basic information on them has long been accumulating, both as historical records and as herbarium collections. The few existing general statements of the story have exploited only a small part of this fund and have made no attempt to combine botanical and ethnological evidence.

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I. HISTORY OF CULTIVATION AND USE

The imperfectly known culture history of the grain amaranths will be followed in geographic sequence through four continents. The trail begins very faintly among the Indians of the southwestern United States, becomes gradually more distinct through northwestern Mexico as the great central Mexican stronghold of the crop is approached, and gradually fades again in southern Mexico. A small isolated center is found in Guatemala, and a larger one in the Andes extending from Peru through Bolivia into northwestern Argentina. On the other side of the Pacific an indistinct trail runs from Manchuria through interior China to a major center in the Himalayas and disappears gradually into Afghanistan and

Persia. There is a small outpost in southern India and Ceylon. Finally, there are vague traces of the crop in Africa.

UNITED STATES

The role of grain amaranths among the Indians of the United States is an unsolved puzzle. The enormous literature on aboriginal cultures contains only a few hints and fragments of information suggesting cultivation of the plants.

Caches of seeds identified as amaranths have turned up in various archaeologic sites, such as Snaketown in Arizona (Castetter and Bell, 1942, p. 35) and the Bluff-Dwellings of the Ozarks (Gilmore, 1931, p. 97). The Ozark material was identified for Gilmore by Safford, who ventured no guess as to whether the amaranth seeds were from cultivated plants (Jones, letter[1]). In his published report on this material, Gilmore surmised that the plants were cultivated, but in 1936 in a letter to Edgar Anderson he wrote that this was doubtful. It is well known that, in recent times and presumably in the past, a great many American Indian tribes gathered wild amaranth seeds along with almost everything else fit to eat in their regions. Unfortunately, the seeds of cultivated and wild amaranths are often indistinguishable, so that the prehistoric seed caches are inconclusive as evidence on the question of cultivation. Volney Jones informs me that all of the archaeologic seed finds he has seen, including the Snaketown material, are so small that they probably represent wild plants.

There are some puzzling historical records which report grain amaranths in the Southwest. In 1875 a new species, *Amaranthus leucocarpus*, was described on the basis of plants grown at Harvard from a mixture of various seeds collected in Arizona by J. W. Powell (Watson, 1875, p. 347). The only information accompanying the description was that the seeds were used by the Arizona Indians for food. The seeds are light-colored and therefore almost certainly from a cultivated plant; I know of no example of a wild or weed amaranth with pale seeds. Although Powell had traveled widely in the Southwest prior to 1875 he worked mostly in northern Arizona, so it seems likely that he collected the seeds there. They may have been grown by the Paiutes. Edward Palmer, a contemporary of Powell, wrote (1878, p. 603) that the Paiutes regularly cultivated two species of amaranth, one of which was *A. leucocarpus;* they called the plants *camoot*, and made a bread or mush from the meal. Some later writers made cryptic statements that the Arizona Indians cultivated amaranths for seed (Watson, 1880, p. 41; Uline and Bray, 1894, p. 314), but gave no details.

Various of the southwestern Pueblo peoples still cultivate amaranths as dye plants but make no use of the seeds (J. D. Sauer, in press). Ethnically and botanically, this crop seems to be distinct from *A. leucocarpus* and will not be discussed here.

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[1]Complete names and addresses of persons providing unpublished data are cited in the List of Sources at the end of the paper.

MEXICO

Hernán Cortés, writing the second letter to his king on the conquest of Mexico, recorded what may have been the first European contact with grain amaranths. He wrote that the heathen idols of the Aztecs were made of a dough of various seeds, milled and kneaded with the blood of human sacrifices (1520, p. 33). Cortés attempted no identification of the seeds included in the recipe, but there is reason to believe that grain amaranths were an essential ingredient.

It has been known for a long time that the ancient Mexicans made idols of a dough called *zoale* and that this dough was made from the seeds of an important crop plant called *huauhtli* by the Indians and *bledo* by the Spanish colonists. The botanical identity of this crop remained a mystery until the 20th century. Gallatin (1845, p. 117) mentioned the crop but was unable to imagine what it might have been. He wrote: "I cannot discover what is meant by *guatli*. It is interpreted as being *semilla de bledo*, but I am not aware of any other native grain than maize having been an article of food of such general use, as the quantity mentioned seems to indicate." Payne (1892, 1:354) believed *huauhtli* was a cereal grass and called it "wheat of Michoacan." Bourke (1892, p. 522) came to the bizarre conclusion that *huauhtli* must have meant tule pollen. Finally, Urbina (1903, p. 589) and Safford (1917, p. 290) decided that *huauhtli* was a grain amaranth and most later investigators have agreed with them (Bukasov, 1930, p. 504; Matschat, 1935, p. 26; Martínez, 1936, p. 24; Carl Sauer, 1936, p. 290; Caso, 1937, p. 46; Nuttall, 1937, p. 19; notations by Nicolas León in 1938 edition of Sahagún, 3:338, 364; Anderson and Barlow, 1943, p. 416; Hendrichs, 1945, 1:236).

PROBLEM OF BOTANICAL IDENTITY OF HUAUHTLI.—

A few recent workers have dissented from the majority interpretation and have suggested that *huauhtli* was a grain chenopod (Emmart, 1940, p. 321; Hunziker, 1943b, p. 319; Reed, 1944, p. 211). This possibility requires serious consideration. At the present time, the Mexicans cultivate some chenopods which look so much like grain amaranths that the two are often confused by casual observers. Modern records of the two crops can usually be clearly separated on the basis of recent herbarium specimens, photographs, and trustworthy field observations. However, the story of these plants cannot be traced very far without leaving the firm ground of certain identification.

Many of the relevant modern records and practically all of the older accounts were written by persons who knew little botany and used popular rather than scientific names. Only one of the early accounts (Hernández, ca. 1575c—see Appendix—D) gave Latin generic names for *huauhtli;* unfortunately, it was written before the time when such names had a consistent and definite meaning and in different passages *huauhtli* was identified as both *Atriplex* and *Blitum*, names which suggest both chenopods and amaranths.

The occasional plant descriptions in the old accounts are almost useless in identification; some mentioned plant color, but both amaranths and chenopods

may be green or reddish. The few references to seed color give a better clue. Some of the chenopods and amaranths grown in Mexico today have dull whitish seeds, but many of the chenopods have dull reddish seeds and many of the amaranths have shiny black seeds. I know of no cultivated red-seeded amaranths or black-seeded chenopods in Mexico. Sahagún (ca. 1570b—see Appendix—C) reported ceremonial use of whitish, red, and black *zoale* or paste of *bledo* seed. Pomar's report (1582—see Appendix—F) of two kinds of *huauhtli* seed, one like a flattened turnip seed and the other smaller and white, also suggests that both chenopods and amaranths were involved.

The best clues in the early literature to the identity of *huauhtli* are the crude drawings in two 16th century writings (Sahagún, ca. 1570a; Hernández, ca. 1575b). Sahagún's drawings show definitely that he applied the name *huauhtli* or '*vauhtli*' to more than one kind of plant. Some with dentate leaves (pl. 10 A-B) appear to be chenopods; others with entire leaves (pl. 10 C-D) look much more like amaranths. Hernández used a single illustration, apparently of a chenopod, but his text explains that he considered *huauhtli* a general term for a group of different plants, some used for grain, some for green vegetables, and some just weeds (see Appendix—D).

The Indians themselves probably used the name *huauhtli* for a variety of plants, grown for different purposes. Some of the compound names may well have been restricted to particular species. *Xochihuauhtli* (flower *huauhtli*) may have meant a chenopod whose inflorescences were cooked in the bud stage as a green vegetable as is commonly done in modern Mexico. *Nexhuauhtli* (ash *huauhtli*), like the common Spanish word for chenopods, *cenizo,* probably referred to the whitish appearance of some chenopods. *Tlapalhuauhtli* (red *huauhtli*) might have meant either a red-seeded chenopod or a red-leaved amaranth; similar names are used ambiguously for both plant and seed color by Mexicans at present. *Michihuauhtli* (fish *huauhtli*) and *tezcahuauhtli* (mirror *huauhtli*) probably referred to light- and dark-seeded amaranths, respectively, the former with pale seeds like little fish eggs, the latter with shiny black seeds.

Information on these specific plants would be required to determine which were grown as grain crops. Unfortunately, the early accounts ordinarily used the simple name *huauhtli* with no prefix. Only *michihuauhtli,* which seems to have been an amaranth (pl. 10 C), was definitely regarded as a grain crop (Hernández, ca. 1575c—see Appendix—D; Pomar, 1582—see Appendix—F). Hernández has a rather ambiguous statement which implies that the seeds of *tlapalhuauhtli* and *nexhuauhtli* were also used.

There is another approach to this question, beyond the direct but hardly satisfactory internal evidence of the historical records; that is by comparison of the grain *huauhtli* picture with the distribution, uses and popular names of chenopods and amaranths grown in Mexico today.

The chenopod enthusiasts rest their case primarily on the cultivated species, *Chenopodium Nuttalliae* and *C. pueblense,* which they regard as surviving relics of

the once great grain crop (Emmart, 1940, p. 321; Hunziker, 1943b, pp. 319–322; Reed, 1944, p. 211, 1950, p. 139). It is assumed that a modern name, *huauhzontli*, sometimes reported for these plants, is derived from *huauhtli* (Robelo, 1904, p. 577). Actually *huauhzontli* may be a corruption of an entirely different word, *cuauhzontli*, which can be found in various early and recent writings and which I have often heard given to cultivated chenopods in modern Mexico.

In any case, the great weakness of the argument for chenopods as the major component of the ancient *huauhtli* crop is the poor correspondence between their present distribution and uses and the historical record of grain *huauhtli*. The ranges of the two overlap, but the coincidence is scarcely impressive. Cultivated chenopods have been found in the Federal District, the states of México, Guanajuato, Michoacán, Puebla, Oaxaca, Vera Cruz, and Tamaulipas (Safford, 1918, p. 524; Reed, 1944, p. 211; collections by Kelly, Carl Sauer and myself). This range excludes various states where *huauhtli* was an important crop and includes three states where the ancient grain crop was never reported.

The known uses of *cuauhzontli* bear little resemblance to the ancient uses of grain *huauhtli*. We shall see that *huauhtli* grain was commonly prepared for use simply by toasting. Powdered and stirred into water, the seeds made a drink which was considered delicious even by the early Spaniards. Mexican grain amaranths are quite palatable when toasted, but all the *cuauhzontli* seeds I have sampled have an extremely nasty bitter taste, which is not improved by toasting. They probably contain the same bitter substance present in the Andean *Chenopodium quinoa*. *Quinoa* grain is considered inedible when raw and is prepared for use by long boiling in many changes of water (Cook, 1904, p. 492). Chenopods are ordinarily cultivated in Mexico today not as grain crops but as green vegetables. The original account of the species *C. Nuttalliae* (Safford, 1918) reported that the immature tops of the plant were cut when in bud, dipped in batter, and fried. The only cultivated chenopods cited by Reed (1944, p. 211; 1950, p. 141) were used in exactly the same way. These plants have been collected by Isabel Kelly, Carl Sauer, and myself at seven other places in Mexico and in all cases the use was identical.

There is one Mexican state in which the seeds of *cuauhzontli* are known to be used as food. Hernández X. wrote me that in Michoacán the seeds of *C. Nuttalliae* are sometimes milled for tamales, although the plant is normally grown as a green vegetable. West (1948, p. 42) reported that white, black, and red-seeded amaranths are used as grain in Michoacán; all three are planted and harvested together and the seeds separated according to color only after threshing. Both the black and red seeds are usually milled for tamales. West has permitted me to grow his seed collections; of these the black and white seeds were all amaranths but the single collection of red seeds turned out to be a chenopod. West worked in this area in the dry season before planting time and had no chance to observe the plants, but he believes that all the red-seeded "amaranths" may turn out to be chenopods. Outside of Michoacán, grain chenopods seem to be unknown in Mexico today.

In contrast, the present range and uses of grain amaranths are strikingly like those of grain *huauhtli*, and the case for amaranths is strengthened by the records of popular names. It seems significant that the early writers consistently identified grain *huauhtli* as *bledo*, the ordinary Spanish name for amaranths, rather than as *cenizo*, the ordinary name for chenopods. For example, Sahagún (ca. 1570b, see Appendix—C) wrote that *huauhtli* was *bledo*, but that it was similar to *cenizo*. He identified only *huauhtli polocayo*, whose seeds were used as a starvation food, as *cenizo*. Slight variants of the words *huauhtli* and *zoale* have persisted in a few parts of Mexico as names for grain amaranths. In most of the country the name *huauhtli* has been gradually replaced by synonyms and is no longer applied to any plant.[2] The various synonyms can be traced down through the historical records as a continuous chain and finally tied to the present-day names of grain amaranths.

The details of the story appear in the following historical review. The individual pieces of evidence are often ambiguous and fragmentary, but they combine to give a strong impression that most of the writers were recording a single great grain crop, strikingly uniform in names and uses throughout its wide range. In some areas, we can be reasonably certain that this crop was a grain amaranth, pure and simple. In other areas, it may have been a complex of amaranths and chenopods, mixed in names, cultivation, and use as they seem to be in Michoacán at present. If so, the two plants have probably been so confounded that their stories may never be disentangled, and we can only hope that the confusion is confined to a fraction of the records. It seems almost inconceivable that plants which have left so faint a trace as the grain chenopods were more than a local and minor component of the great *huauhtli* crop.

HISTORY OF CEREMONIAL USE.—

Pre-Conquest.—The strange idols, great temples, and barbaric rituals of the pre-Conquest Mexicans fascinated many of the early chroniclers, particularly the priests. They gathered a wonderful amount of detailed information on heathen ceremonies and wrote long descriptions which contain much information on ceremonial plants.

One of the oldest and most copied documents on Aztec ritual is the so-called 'Ramírez Codex,' which describes the May festival honoring the war god, Huitzilopochtli (Anonymous, ca. 1550, pp. 128–135). The festival was observed throughout the empire, but the chief ceremony was at the temple pyramid in Tenochtitlán, the capital. The whole city attended, all the state and temple officials dressed in ceremonial garlands, feathers, and colored robes, according to rank. The intricate ritual involved dances, processions, singing, much noise of flutes, shell-trumpets, and drums, and human sacrifices in greater number than on any

[2] *Huauhtli* means nothing but fish eggs or insect eggs to most Mexicans at present. This two-fold meaning, apparently based on the roe-like appearance of chenopod and amaranth seeds, can be found in the earliest chronicles.

other day. The focus of all the activity was a huge idol of the god made of dough, as large as the regular idol of wood. The temple maidens, two days before the festival, had "milled a quantity of seed of *bledos* together with toasted maize, and after it was milled, kneaded it with honey, and made of that dough an idol." (See Appendix—B). The idol was carried on a litter in a great procession through the capital and the suburbs and then returned to the temple. At the close of the ceremony it was broken up, with other chunks of the same dough, and all the pieces were consecrated as the bones and flesh of Huitzilopochtli. The pieces were handed out to the populace and were eaten in communion with reverence, fear, and tears. On this day "it was a strictly observed rule in all the land that no other food was to be eaten except that dough with honey of which the idol was made. All those that participated were obliged to give a tithe of that seed of which the idol was made."

One of the most magnificent of the early chronicles was written about 1570 by Sahagún. This Spanish Franciscan compiled a monumental record of the language, beliefs, and ancient customs of the Indians of central Mexico, drawn from years of discussion and collaboration with groups of Indian informants. Over and over again Sahagún mentioned a ceremonial paste called *zoale*, or "*tzoalli*," made of seeds of *bledos*. Idols of *zoale* appeared in at least seven regularly scheduled ceremonies and various irregular observances scattered through all seasons of the year (see table 1). Most of these rituals culminated in a ceremonial breaking and eating of the idols.

Sahagún confirmed the 'Ramírez Codex' account of a great idol made of *zoale* for the May festival to Huitzilopochtli, and described an almost identical ceremony in November:

> "They took seeds of *bledos* and cleaned them very well, removing the chaff and eliminating other seeds which they called *petzicatl* and *tezcahuauhtli*, and they milled them carefully, and after having them milled, the flour being very fine, kneaded it into dough of which was made the body of Huitzilopochtli" (see Appendix—C).

Sahagún identified *petzicatl* as the black seed of a plant called *quiltonilli*, which was sometimes cooked for greens. It and *tezcahuauhtli* may both have been weed amaranths (pl. 10 D-E). *Quiltonilli* is a common name for weed amaranths cooked for greens in central Mexico at the present time. This reference is of particular interest in suggesting that cultivated *huauhtli*, like most modern grain amaranths, was pale-seeded and, therefore, readily distinguishable from the dark-seeded weed amaranths. Sorting out the pale seeds from the dark seeds accidentally mixed in during the harvest is still common practice.

Zoale was not only used to make the idols of Huitzilopochtli but was also fed to slaves about to be sacrificed to that god. In a final midnight ceremony the temple fire was put out and in the darkness each slave was given four mouthfuls of a soup of *zoale* (see Appendix—C).

TABLE I

AZTEC FESTIVALS INVOLVING *HUAUHTLI* OR *BLEDO*, ACCORDING TO SAHAGUN (CA. 1570)

	Aztec month	Gods honored
February	1	
	2	
March	3	
April	4—ueytozoztli	Chicomecoatl, goddess of crops
	5—tóxcatl	Huitzilopochtli (Tlacauépan), war god
May	6	
June	7	
	8	
July	9	
August	10—xócotlhuetzi	Xiuhtecutli, god of fire
	11	
September	12	
October	13—tepeilhuitl	Tlaloques, rain gods
	14	
November	15—panquetzaliztli	Huitzilopochtli, war god
December	16—atemoztli	Tlaloques, rain gods
	17	
January	18—izcalli	Xiuhtecutli, god of fire
Variable date		Macuilxochitl (Xochipilli), flower god
		Omacatl, god of feasts

The fire god, Xiuhtecutli, was also honored by a formal and bloody ceremony, that of *xocotlhuetzi*. This also involved an idol of *zoale*, with *tortillas* of *bledo* seed on its head, which was tossed down from a tree, with the people scrambling for pieces (see Appendix—C). A slightly later chronicler, the Dominican friar Durán, attributed this festival to a non-Aztec group, the Tepanecs of Coyoacán:

> "The day of their festival they made a bird of dough of *bledo* seed which we have called *tzoally*, which dough perpetually served them for effigy of idols and flesh and bones of their gods, that dough to be eaten afterward." (See Appendix—E).

Sahagún described another annual festival to the fire god in which amaranths may have been used, that of *izcalli*. All the women made *tamales* of *huauhtli*, or *huauhquilitl*, which they offered in the temple and in home ceremonies and also placed on the graves of their dead (see Appendix—C). These ceremonial *tamales* may have been made from vegetative parts rather than seeds. Sahagún identified *huauhquilitl* as *bledos* eaten as cooked greens and illustrated the young seedlings being gathered below a mature *huauhtli* plant (pl. 10 F).

The Tlalocs, mountain and rain gods, were honored by the formal ceremony of *tepeilhuitl*, by the milder household ceremony of *atemoztli*, and in irregular individual offerings when the weather required them (see Appendix—C). In all these rain rites, the centers of attention were anthropomorphic figures of the mountains fashioned of *zoale*. Sometimes *zoale* was also made into votive *tortillas* and smeared on tree roots and branches to represent snakes. Pomar (1582, p. 15) reported similar offerings to the Tlalocs at Tezcoco.

In the festival of *ueytozoztli*, an idol of the crop goddess was made of *zoale*. All the women presented ears of maize to her for blessing and took them home to keep for seed for the next year. She received offerings of maize, beans, and chia, because "she was the creator and giver of those things that are the sustenance of human life" (see Appendix—C). This ritual is strikingly like one practiced by the Tarascans in Michoacán, far beyond the limits of the Aztec empire (fig. 1). The Tarascans too had an earth goddess who was considered the mother of all the gods and the giver of grains and seeds (Anonymous, ca. 1540). For her festival at Tzintzuntzan, they made little figures of animals, called *tuycen*, of bread of *bledos*. When the Spaniards first came, the Tarascans called them gods and they called their horses *tuycen* (see Appendix—A).

Figures and offerings of *zoale* appeared again during the occasional festivals for the god of flowers and the god of feasts. Some persons mixed the flour of *bledo* seed with honey and meal of toasted corn for their offerings (see Appendix—C).

Finally, there was the new fire ceremony, held at the close of each 52-year calendar cycle. This rite insured the return of the sun for another 52 years; otherwise, the sun and earth would perish and horrible creatures would descend from the sky to devour all the people. A slow procession of priests, dressed as gods, marched to a particular hilltop, followed by an awed and silent multitude. There the new fire was kindled in a midnight ceremony. Torches lighted from the flame were carried by runners to all the waiting villages where people were gathered on the hills and house-tops watching for the first glimpse of light in the distance. When the torch-bearer arrived, everybody relit their fires, all of which had previously been put out. Their joyful celebration culminated in eating "*tzouatl*, which is food made of *bledos* with honey" (see Appendix—C).

Many other accounts of pre-Conquest ceremonies mention use of *huauhtli* or *bledos* (Durán, ca. 1580; see also Appendix—E; Acosta, 1591, p. 234; Torquemada, 1615, pp. 71–89; Serna, 1656, pp. 320–321, 357; Vetancurt, 1698, p. 86; Bancroft, 1875, 3:323; Bourke, 1892, pp. 523–525; Safford, 1917, pp. 286–289; Seler, 1927, p. 190; Bukasov, 1930, p. 149; Matschat, 1930, p. 26; Martínez, 1936, pp. 27–29). All these appear to be derived, directly or indirectly, from the 'Ramírez Codex' or Sahagún and will not be discussed here.

Colonial Period.—After the Conquest, ceremonial use of *zoale* was undoubtedly gradually suppressed by the church in its battle against heathenism and idolatry. Stubborn resistance by at least a few of the Indians is revealed by the writings of two 17th century priests. In 1629 Ruíz de Alarcón bemoaned the continuance of

idolatry in the Atenango district of Guerrero. His Indians persisted in making offerings to the devil with the first fruits of the *huauhtli* harvest; they milled these seeds and kneaded the dough into little idols of *zoale*, which they broke and ate in what seemed to the Spaniards a satanical parody of holy communion (see Appendix—H). Similar deviltry near Çumpahuacán in the Valley of Mexico was revealed "by confessions of certain delinquents" (Serna, 1656; see also Appendix —J). In various pueblos some old men retained the office of starting the new fire, and had preserved this great pre-Conquest ritual into the 17th century, complete with offerings of "*zoales*, which is a seed of *bledos*."

Recent.—Shortly before 1900 Lumholtz (1902, 2:47–50) visited the remote Huichol village of Haiokalita in the mountains of northern Jalisco and watched these primitive Indians celebrate their greatest feast of the year. Although he did not realize it, Lumholtz witnessed a ritual which was in some ways strangely like those practiced far off in central Mexico more than 300 years before:

> "In front of the drum was spread a blanket, and on this a great number of cakes were deposited, shaped to represent animals, such as the deer, turkey, rabbit, etc. They are made from a certain seed, which is ground and mixed with water. The seed, and the plant from which it is obtained, are called *uã-të*; being yellow, it belongs to the god of fire. The tribe probably made use of this grain before they had corn. At present it is used chiefly for ceremonial purposes, except when the corn runs short. No one is permitted to eat it until the race is over."

The festival culminated in a ceremonial race for life; as each runner finished, he pierced a cake animal with a straw and handed it to one of the elders, who "in eating it secured health and life for all." *Wã-vë* was cultivated on a small scale by the Huichols and Lumholtz recognized it as a species of amaranth.

Farther south in Jalisco, where out-and-out pagan rituals have long since disappeared, grain amaranths have slipped into Christian ritual. In the late 19th century Edward Palmer visited an Indian village near Guadalajara and saw rosaries made of little balls of amaranth dough, called "*suale*", wrapped in maize husks (Safford, 1917, p. 293). In 1947 at Tlajomulco, another village not far from Guadalajara, we talked to a woman who was growing grain amaranths. She and her friends were accustomed to toast and mill the seed to make dough, which they called *zoale*. They made the dough into little ceremonial cakes and rosaries for something called the Feast of the Cat on December 8th.

The Tarascans of Michoacán, who made *tuycen* of *bledo* seed in pre-Conquest times, seldom use amaranths in ceremonies today, but in a few villages they make special *tamales* and *atoles* of black amaranth flour mixed with black corn meal for the maize planting and harvesting festivals (West, 1948, p. 42).

In the heart of the old Aztec Empire, no tangible vestiges of the once enormous ritual significance of *huauhtli* are known to remain. As will be discussed in the next section, the main modern use of grain amaranths in this region is for *alegrías*, little cakes of popped seed bound with syrup. These are in large part simply commercial confections, but for some reason they become particularly abundant and conspicuous on special saints' days.

HISTORY OF CULTIVATION AND ECONOMIC USE.—

The story of ritual use of *huauhtli* shows more clearly than any other evidence how deeply these plants were embedded in the memories and lives of various Mexican tribes. This is only part of the complete picture; beneath the colorful ritual usage lay a massive foundation of everyday practical use of the plants. This usage, not clearly the work of the devil, was largely ignored by the early Spanish writers; fortunately, it was recorded by the Mexicans themselves. Some of the Mexican hieroglyphic codices from before and after the Conquest are still in existence. As their deciphering has progressed, there has been gradual realization that they record not only rituals and myths, but also a great deal of historical fact (Caso, 1949, p. 145).

Pre-Conquest.—Some of these records were exploited very early by the native historian Tezozomoc (ca. 1598). His history of the Aztecs before the Conquest undoubtedly involves errors and fantasies, but its credibility probably differs only in degree from most ancient history. Tezozomoc described the centuries of tribal wanderings down from the Northwest until the final settlement at Tenochtitlán. The tribe settled at many places and planted and harvested their crops, often remaining for many years until their god Huitzilopochtli bade them move on. Even in the earliest legendary times, *huauhtli* was among their crops; being light, the seed was carried by the boys whenever the tribe migrated (see Appendix—G). When the tribe settled at Xaltocan, *huauhtli* was sown in beds in the lake, like the "floating gardens" at San Gregorio Atlapulco in which amaranths are grown today. Acosta (1591, pp. 303–304) recounted another Aztec legend from these early times: Huitzilopochtli helped the tribe pay a crushing tribute, including *bledos*, to the king of Atzcapotzalco.

Tezozomoc narrated mostly events of the 15th century. When the Aztecs conquered the Tepanecs of Coyoacán, the vanquished tribe ran up on a hill and shouted down pleas for mercy, promising all sorts of tribute, including *huauhtli* "for your sustenance" (see Appendix—G). During the reign of the first Moctezuma (spelled Montezuma in popular English writings) and his successor, Axayacatl, both pale- and dark-seeded *huauhtli* was stocked in the imperial larder and was given as a reward, "with the other things pertaining to the necessities of their houses," to persons who had earned the gratitude of the emperor (Tezozomoc, ca. 1598, pp. 152, 161, 237). Later in the century, *huauhtli* was stated to be one of the four food crops of the Matlazincas in the valley of Toluca and was supplied as food to a Mexican colony at Teloloapan in Guerrero by the neighboring pueblos (see Appendix—G).

A wealth of definite information on the Aztec Empire just before the Conquest is available in Moctezuma's tribute list, the famous hieroglyphic 'Matricula de Tributos.' From this document Barlow (1949) has mapped the provinces of the empire and summarized the tribute levied on each province. *Huauhtli* was collected from all but three of the twenty provinces which contributed food staples. Each

of these seventeen provinces filled at least one granary with *huauhtli* every year, and some were required to fill two. A single granary is believed to have held about 10,000 bushels of seed (Gallatin, 1845, p. 117; Safford, 1917, p. 286; Bukasov, 1930, p. 149; Anderson and Barlow, 1943, p. 416). Thus the annual levy of these tiny seeds added up to something like 200,000 bushels, a staggering total not far exceeded by any foodstuff. Computed on the same basis, the maize tribute was about 280,000 bushels and the bean tribute about 230,000 bushels. It is obvious from these figures that *huauhtli* was one of the great basic food crops of the empire.

The provinces submitting *huauhtli* tribute cover the heart of the empire (fig. 1A). It may be significant that some provinces in the present states of Puebla and Oaxaca contributed maize and beans but not *huauhtli*. No significance can be attached to the absence of *huauhtli* in the tribute of the rest of the empire, since the more distant provinces did not contribute basic foodstuffs of any kind.

Colonial Period.—For a long time after the Conquest, the Spanish chroniclers seem to have completely ignored the more prosaic aspects of this great crop. Núñez Cabeza de Vaca (1555, p. 513), who had made a fantastic journey through the far northwest of Mexico in the 1530's, made a puzzling statement that "the coast has no maize and they eat powder of *bledo* and of straw and of fish." This cryptic remark has sometimes been taken as a reference to cultivated grain amaranths, which have been reported from this general area in recent times. However, it seems probable that in this particular passage Cabeza de Vaca was describing the territory of the non-agricultural Seri tribes (Carl Sauer, 1932, pp. 16–17). If so, the "powder of *bledo*" may have been made from wild amaranth seeds.

The first definite post-Conquest record of *huauhtli* as a crop and everyday foodstuff was made by Sahagún. There is some evidence that Sahagún's original manuscript contained an extensive account of cultivation and use by the Aztecs of *huauhtli* and other crops. This section is not included in any of the available versions of the work. However, in another section Sahagún reports *huauhtli* among the staple food crops of two non-Aztec peoples: the Matlatzincas of Toluca and the Tarascans of Michoacán (see Appendix—C).

Francisco Hernández, contemporary of Sahagún and physician to the King of Spain, spent several years in Mexico preparing a catalogue of its natural history. His completed manuscript has been lost, although modified abstracts of it prepared by Ximénez (Hernández, ca. 1575a) and Recchi (Hernández, ca. 1575b) are preserved. Probably the most authentic version, quoted here, is that published by Ortega (Hernández, ca. 1575c) from the original rough draft, rediscovered in the 18th century. Hernández wrote that there were many kinds of plants called *huauhtli*, some wild, some carefully cultivated in the gardens of the Mexicans (see Appendix—D). He mentions various long Indian names applied to particular kinds, but makes no clear distinction between them other than coloration. The only use mentioned for most of the kinds was as boiled greens; some of these were probably chenopods, as has already been mentioned. However, from the seeds of

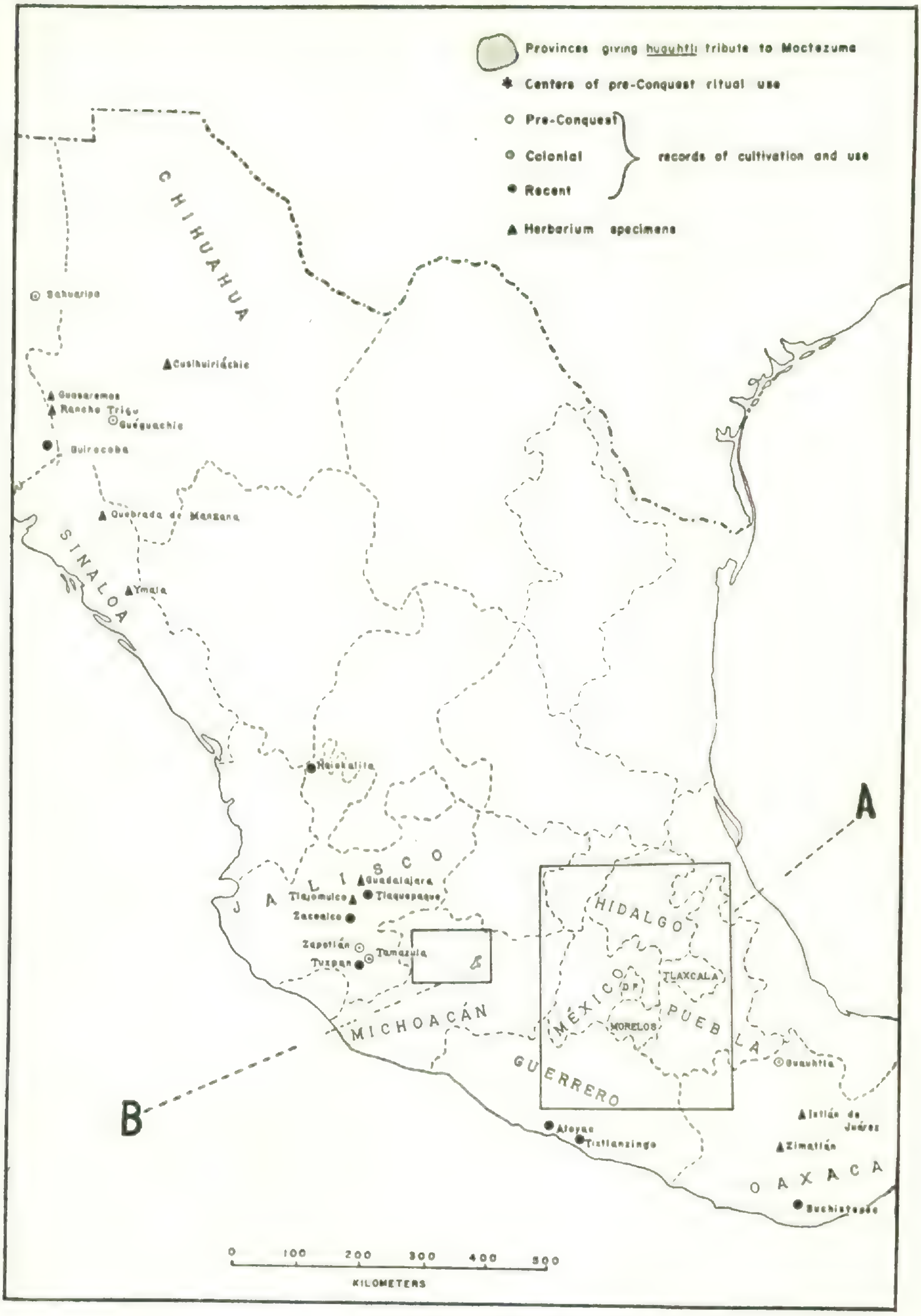

Fig. 1. Mexico: Localities and regions where grain amaranth cultivation is indicated; enlargements of squares A and B on opposite page.

Fig. 1A. Enlargements of squares shown on fig. 1.

a few kinds of *huauhtli,* the Mexicans prepared little balls and an *atole* which was used as a very pleasant drink; the *atole* was made from the toasted and powdered seed of red or varicolored *Blitum,* the Latin equivalent of *bledo,* mixed with water and maguey syrup (see Appendix—D).

Shortly after Hernández finished his work, the famous *relaciones* began to appear, in response to the royal inquiry of 1577. These documents often included, among many other things, a listing of local crops. Only a limited number of these *relaciones* have been published and are available to me, but they show clearly that *huauhtli* was still important over a large part of Mexico a half century after the Conquest. *Huauhtli* or *bledo* seed appeared repeatedly among the three or four standard food crops of particular pueblos; at some it was described as an ancient crop or one which they have "always" had (see Appendix—F). One mention of seeds of "*quilites*" probably also refers to grain amaranths; this corruption of an old Nahua word for herbs in general was adopted by the Spanish very early as a synonym for *huauhtli* (Hernández, ca. 1575a, p. 235) and is a common name for amaranths in modern Mexico.

Most of the *relaciones* merely confirm the persistence of the crop in the old *huauhtli* tribute area (fig. 1), but two report *huauhtli* cultivation far to the southeast at Chila and Guauhtla, along the Puebla-Oaxaca border, and another gives it as one of the two main crops at Xonotla, far off to the northeast, nearly on the border of Vera Cruz (see Appendix—F). Another *relación* of this same period, unpublished but quoted by Carl Sauer (1948, p. 75), lists *zoale* among the major crops at Zapotlán and Tamazula, far to the west in present-day Jalisco.

The *relación* of Tezcoco reports in more detail the same uses described by Hernández: dark *huauhtli* seeds were milled for a dough to be made into tortillas or rolled into little balls, which were wrapped in maize leaves and boiled; the whitish *michihuauhtli* seeds were used in the same way and also toasted and milled for a sweet drink (Appendix—F).

Fifty years later, cultivated *huauhtli* was observed around Atenango in Guerrero (Ruíz de Alarcón, 1629). Here again the seeds were made into little *zoale* balls, cooked like *tortillas,* and made into a drink (Appendix—H). Toward the end of the century, Vetancurt ,1698, p. 45) wrote an apparently garbled and secondary account in which amaranths, chenopods, and salvias are confused. This account mentions the same sort of uses and is of interest mainly because it contains the first available mention of the name *alegría* in connection with *huauhtli.*

The final records available from the colonial period are from far off in northwestern Mexico. One document described the crops of the Jovas, who lived near Sahuaripa in Sonora (Anonymous, ca. 1760). These Indians grew a plant, known to them as *coguet,* to the Mexicans as *zoale,* which had a pale seed like *quelite* (see Appendix—K). The seeds were prepared for eating by submerging them in the river in a basket and stamping on them under water until they burst; they were then toasted, milled, and stirred into cold water to make a refreshing drink. The other document is an unpublished manuscript on the isolated Tarahumare pueblo

of Guéguachic in Chihuahua (Anonymous, 1777). These primitive Indians sowed a seed resembling sesame which they called *oguigui* and the Mexicans called *alegría*. It was planted in August in the warm gorges and harvested in November. "When toasted it pops and swells greatly, and is of very good flavor." The popped seed was eaten dry or milled and mixed with water for a drink (see Appendix—L).

Recent.—In the 1890's the Mexican government sent out an agricultural questionnaire, which, like the royal inquiry of 1577, requested a listing of local crops. A comparison of the replies to these two inquiries shows that the three intervening centuries brought many changes in Mexican crops, none more striking than the decline of grain amaranths. The replies to the later inquiry cover a great number of pueblos, including some where *huauhtli* was a major crop about 1580. Although the crop lists are often quite long, not a single one mentions grain amaranths (República Mexicana, Secretaría de Fomento, 1893–1895).

Planting and use of *huauhtli* was one of the ancient practices which suffered most heavily in the general disruption of Indian cultures. The very importance and ceremonial value attached to the plant in the old days worked against its survival by making it a symbol of paganism in the eyes of the church. The decline of the crop was reflected by its increasing rarity in late colonial records; by early post-colonial times it seems to have disappeared completely from written history.

In modern times, with the beginning of intensive botanical and ethnological field work, grain amaranths have been rediscovered in many parts of Mexico. Although reduced to an inconspicuous relic of the once great staple, the crop has been conserved by a surprisingly large number of Mexican communities. Sizeable fields of amaranths are planted by only a few pueblos today; generally a few plants are sown near the houses or scattered through the maize fields; often only a small minority of the families still grow them.

A crop grown on such a small scale can easily escape notice, even in a fairly careful field investigation. We occasionally found persons who had patches of amaranths in pueblos where other inhabitants had said, and probably believed, that none were being grown. Although the crop has undoubtedly disappeared in many communities, it probably persists in many more than are indicated by the known present distribution (fig. 1). On a trip through Mexico lasting only a few weeks, we found cultivated amaranths in several areas where they had not been previously reported. Additional field investigation could be expected to round off and fill in the distribution pattern. For example, it is quite possible that there are spots of amaranth cultivation scattered along the almost unexplored western Sierra Madre, which would link the apparently isolated northwestern centers to the main range. However, there is no reason to expect grain amaranths to turn up very far outside the known range; most of the large blank areas on the map persist in spite of traverses by persons interested in the plants.

For convenience, the post-Colonial records will be discussed by states.

Federal District, State of Mexico, and Morelos.—Grain amaranths remain a more important crop in this area, the heart of the old Aztec Empire, than in most of the rest of Mexico. Some pueblos continue to make large-scale plantings, mostly to supply the demand for the popped *alegría* confections. Almost any kind of amaranth seed will pop when toasted, but the kind grown in this region puffs up to an unusually large size, suggesting long selection for this character. The practice of using unmilled popped seeds cannot be traced very far back with any certainty, but the seeds have been toasted and presumably popped for as long as there has been any record, so that selection for popping quality may be very ancient.

Detailed accounts of techniques of cultivation and *alegría* manufacture in the state of México were prepared in the 1880's in response to a government request (Granados, Noguerón, and Zarza, 1886). At that time the crop was grown extensively at Cocotitlán and Temamatla and on a small scale at Ayotzingo. Three different kinds of seed were distinguished: *quitlacoche* was small and black and was regarded as an inferior wild kind; *ojo de pájaro* was larger and pale; *cacahuacentle* was the largest and palest. The name *cacahuacentle* is shared with a variety of maize with especially large white kernels (Anderson, 1946, pp. 166–167). All three were often mixed in sowing and harvesting.

Planting began with the start of the rainy season in late April or May. The fields were prepared just as for maize, but instead of being planted along the bottom of the plow furrow, the amaranth seed was sprinkled into a tiny furrow drawn along the plow ridges with a stick, and was lightly covered with a broom. The seedlings were thinned and the excess transplanted, leaving well-spaced pairs of plants. As the plants grew, the earth was hilled up around them by repeated plowing until the stems were covered to a depth of about 30 centimeters. Bloom began in August, and in late October or November the seed-bearing tops were cut and piled in windrows in the fields to dry. After threshing with horses or by beating with sticks, the seed was cleaned by a series of special screens.

The seed was sometimes milled for dough, but the main use was for commercial *alegría* manufacture. The confections were made from December through May, after which the weather became too damp for the sugar binder to hold the cakes together. The seeds were moistened in a clay pot for a few hours and then spread on a cloth until partly dry before they were toasted. The popped kernels were mixed by hand with partly caramelized syrup and spread on a tule mat; the mixture was then compacted "with the greatest violence" into a sheet about 8 centimeters thick, from which little squares were cut with wooden knives. These cakes were sold locally or in the nearby city of Tezcoco.

More recently, the crop was reported a little to the west at Tulyehualco and Milpa Alta (Martínez, 1925, p. 27; Bukasov, 1930, p. 149), and it is extensively grown in this region to the present day (see pl. 11). Cultivation and *alegría* manufacture remain essentially as described in 1886. However, at San Gregorio Atlapulco the seed is often sown in March in the lowland *chinampas*, the so-called

floating gardens; thus the plants are well started before the rains begin, when they are transplanted to the upland fields. We were told that the crop is exhausting to the soil and is usually heavily fertilized and rotated with maize. The seeds, almost all pale, are made into *alegrías* in the individual households; the confections are peddled locally or in nearby towns.

Small-scale amaranth cultivation and *alegría* making are also carried on a little farther north at Chiconcuac and Tultitlán (Kelly, letter) and Zumpango (Hendrichs, letter), and also to the south and west of this region at Chimalacatlán, Tejupilco, Tlatlaya, Tonatico, and Texcaltitlán (West and Weitlaner, letters). At the last three places the seeds are sometimes milled to make dough and *atole*.

Guerrero—Grain amaranths are still sown in the maize fields in the rough mountain country of northern Guerrero, although their cultivation seems to be declining (Hendrichs, 1945, 1:35). Hendrichs wrote me that it is his impression that the custom of sowing a little *alegría* has persisted quite generally throughout these mountains. He particularly remembers the plants at Xochitepec and at Iscateupa, where seeds of *quelites* were an important crop in 1579. The mature inflorescences are cut and threshed on mats; the seeds, mostly pale, are popped over a *comal* and milled in a special non-porous *metate* for *atole* (Hendrichs, 1945, 1:35).

The crop survives in other parts of the state also. Hernández X. found a pale-seeded amaranth in cultivation at Chilapa and collected seed which I have grown. At Xochipala pale-seeded *alegría* is planted in the moist canyon bottoms and the seed is ground and mixed with sweetening to make little balls (West, letter). Weitlaner wrote me that he has unpublished records of *alegría* or *bledo* cultivation at a dozen other Guerrero pueblos, two of which lie well to the south of the old *huauhtli* tribute area (fig. 1). At only a few of these places are the plants carefully cultivated; usually the plants are sown in the maize fields or in newly-cleared ground; at Tlacotepec the plants are said to seed themselves. The seeds, mostly pale but sometimes dark, are commonly toasted over the *comal* and milled for *atole; alegría* confections, sometimes called *palanquetas*, are made here and there; *bledo* seed is milled for *tortillas* at Atoyac.

Tlaxcala and Puebla—All of Tlaxcala and much of Puebla were independent of the Aztec Empire and therefore excluded from the tribute list. However, the 16th century reports of the plants at Gueyapa and Chila and their scattered present distribution (fig. 1) suggest an old and once widespread crop.

In 1947 we saw cultivated amaranths at the Tlaxcalan village of San Miguel del Milagro. Three plant color forms are distinguished but are not kept separate; all are pale-seeded. The plants are started in January or February in seed-beds protected from frost and are transplanted to unirrigated upland fields, either in solid stands or mixed into the maize plantings. The seeds are harvested in September and made into the popped *alegría* confections, especially for the feast of the patron saint, Michael, on September 29.

In 1948 Hernández X. collected a predominantly pale-seeded amaranth cultivated for *alegría* making at another Tlaxcalan pueblo, San Bernabé Amaxac; he has observed cultivation at several other pueblos in the state (fig. 1).

In 1947, travelling south through Puebla, we heard the first rumor of grain amaranths near Huaquechula; *alegría* was said to be cultivated off in the hills at a village called Santa Clara Tetla. Weitlaner has also heard that *alegría* is grown near Huaquechula; at a place called Santiago Tetla the seed is said to be accumulated in quantity in large baskets and made into a confection, called *palanquetas*, with caramel syrup or bee honey.

Later we found a few people growing pale-seeded *alegría* for confection-making at Acatlán; they said that the people of Tehuitzingo also grew the plants. The next year Carl Sauer obtained pale-seeded *alegría* from plants cultivated atTeocuizmanalco in the northern part of the state.

Oaxaca—After the single 16th century report from Guauhtla, Oaxacan grain amaranths seem to vanish from the record until Erwin (1935, p. 661) noticed the popped *alegría* confections for sale in the markets of Oaxaca City. In 1947 we found the confections were still on sale in the city markets; they were made locally from seed said to be brought from Ixtlán de Juárez and Zimatlán. The samples we obtained were mostly pale, but a few dark seeds were mixed in.

We could find no other trace of the plants on a traverse of the state, but a suggestion that they may be scattered through some remoter areas is given by the presence of amaranth cultivation and *alegría* making at San Miquel Suchistepec (Hernández X., letter).

Michoacán—Here in the old Tarascan Empire, the unrecorded story of grain amaranths may have been much like it was in the better-known Aztec Empire. We know that in the 16th century *huauhtli* or *bledo* seed was used ceremonially at Tzintzuntzan and was an important Tarascan food crop. After that the story is lost for centuries until the crop was rediscovered by modern field workers. In its uses and distribution the present crop looks very much like a relic of something more widespread and important.

West (1948, p. 42) says: "The cultivation of amaranth is disappearing among the Tarascans; it would probably die out rapidly if women did not constantly remind men to plant it every year." He found that many pueblos which no longer grow amaranths still use the seed, brought in from mountain villages.

Cultivation continues in quite a few Tarascan and *mestizo* villages (fig. 1). Most of these locations are based on West's records and seed collections, which he has permitted me to grow; the only other recent records are from Cherán and Chilchota (Beals, 1946, p. 52; Weitlaner, letter). I looked for grain amaranths in Tzintzuntzan in 1947, but could find only plants grown as greens or ornamentals.

The Tarascans distinguish varieties on the basis of seed color; they are mixed in planting and the seeds are sorted by color after the harvest (West, 1948, p. 42). Grain amaranths are known as *pari* in Tarascan and as *alegría, bledo,* or *quelite* in Spanish (Beals, 1946, p. 52; Rendón, 1947, p. 223; West, 1948, p. 42). The seeds

are planted in small patches in the house-lot gardens or in the maize fields, particularly in spots where logs have been burned. Sowed in late May, the crop is harvested in November and December; the grain is threshed from the cut inflorescences in open spaces in the fields and stored in small pots (West, 1948, p. 42).

The black seeds are sometimes ground with black maize for *atole* but are mostly used in making *tamales*, locally called *chapatas*. These are made from a mixture of black *bledo* seed, red chenopod seed, and blue or black maize flour; water and sweetening are added to make a dough, which is wrapped in maize husks and cooked in a clay pot (Beals, 1946, p. 52; Rendón, 1947, p. 223; West, 1948, p. 42). Beals also saw *chapatas* made solely of black amaranth dough and brown sugar; the raw paste was spread on banana leaves and eaten at festivals.

The white seeds are mostly popped on a *comal* and made into *bolitas*, sweet confections commonly sold at fiestas, particularly in the mestizo towns (West, 1948, p. 42). Rendón (1947, p. 223) reports that these confections are peddled by the Indians, who make them from the produce of their own plants.

Jalisco—In 1886 Edward Palmer found grain amaranths at Guadalajara and collected herbarium specimens which are still available. The plants were cultivated alone or in the maize fields; the pale seeds were parched and sprinkled with honey to make *alegrías* to be sold in the city market (Watson, 1887, p. 446). At a nearby Indian village, Palmer saw little balls, called "*suale*", made from ground amaranth seed and brown sugar (Safford, 1917, p. 293). At about the same time in a more remote part of northern Jalisco, Lumholtz observed small-scale amaranth cultivation among the Huichols. There the plant and its pale seeds were known as "*wā-vë*." As we have already seen, the seeds were usually eaten ceremonially, but they also served as ordinary food when maize was scarce (Lumholtz, 1902, 2:48).

More recently grain amaranths have been reported from Tlajomulco, Tlaquepaque, Zacoalco, (Bukasov, 1930, p. 149), and from Tuxpan (Weitlaner, letter), a town where *zoale* was a 16th century crop. In 1947 we saw small patches of grain amaranths in house gardens at Tlajomulco. Sown when the rains begin in May, they are harvested in December. The inflorescences are cut, dried in the sun for a few hours and then rubbed between the palms of the hands to free the seeds, which are cleaned of chaff by blowing. The predominantly light-colored seeds are toasted and milled to make *zoale* cakes; these cakes are primarily ceremonial, as has been mentioned, and are of minor importance as food.

Sonora, Chihuahua, Sinaloa—In 1891 Edward Palmer collected specimens of a grain amaranth at Ymala; the plants were called *bledos*, the seeds "*guaute*." The pale seeds were much used for food, particularly when maize was scarce, and the plants were sown or allowed to seed themselves in the maize fields (Safford, 1917, p. 292).

Some puzzling amaranths, perhaps representing a grain crop, were collected by Wislizenus at the remote village of Cusihuiriáchic, Chihuahua, in 1846. For

some reason, Engelmann planted seed of this collection at St. Louis a year later from which he obtained an additional herbarium specimen. These collections are accompanied by no data on habitat or use, but the plants are completely unlike any of the known wild amaranths of this region and almost identical to Palmer's grain amaranths from Ymala.

In the remote canyons of the Sierra Madre off to the west of Cusihuiriáchic, grain amaranths have recently been discovertd by Gentry (1942, p. 108). He collected plant specimens at Guasaremos and Quebrada de Manzana and sent me viable seeds from Rancho Trigo (fig. 1). The plants are cultivated in the house gardens of the Warihio Indians and a few plants are often seen around the houses of the Mexicans (Gentry, letter). The pale seeds are eaten whole or ground into *pinole*, which is mixed with water or milk, sometimes sweetened, to make a drink. The Mexicans call the plants *quelite* or *bledo;* the Warihios call them *weywi.* Carl Sauer recollects seeing large quantities of *bledo* or *guegui* seed stored at Guirocoba, the produce of plants cultivated by the Mayo Indians, neighbors of the Warihio. All the names *(oguigui, guegui, weywi, wã-vë)* for this crop among the various Indian tribes of northwestern Mexico are probably merely variants of a single name.

GUATEMALA

If there are any ancient records of grain amaranths in Guatemala, I have been unable to find them. Even in recent literature, the only published reference to the plants seems to be the single statement that around Cobán the seeds of an amaranth are mixed with brown sugar to make a confection (Standley and Steyermark, 1946, p. 154). The crop is practically unknown to everybody except the Indians who grow it. After travelling halfway across the country and questioning not only Indian farmers but also professional botanists and ethnologists, I had drawn a complete blank and was convinced there were no such plants in Guatemala. Finally the ethnologist Rodas, a Quiché Indian himself, told me about cultivation at San Martín Jilotepeque. On the way out there, the bus driver, a part-time farmer who had driven the route for years, assured me that nobody grew any such plants in that area. When I pointed out some of the big gaudy red plants in the maize fields along the road, he stopped the bus to get out and look at them, and was astonished when the local people confirmed my strange notion that the seeds were good to eat.

I saw grain amaranths at only three places, in the departments of Chimaltenango, Guatemala, and Alta Verapaz, and heard definite reports of cultivation at only two other villages, both in Chimaltenango (fig. 2). Two amaranth specimens from elsewhere in Alta Verapaz may well represent grain plants. They were collected without information on uses, but belong to races ordinarily grown for grain. One, with dark seeds, was found in a maize field at Cubilquitz by von Tuerckheim in 1903; the other with pale seeds was collected in an unspecified habitat near Secanquim by Pittier in 1905.

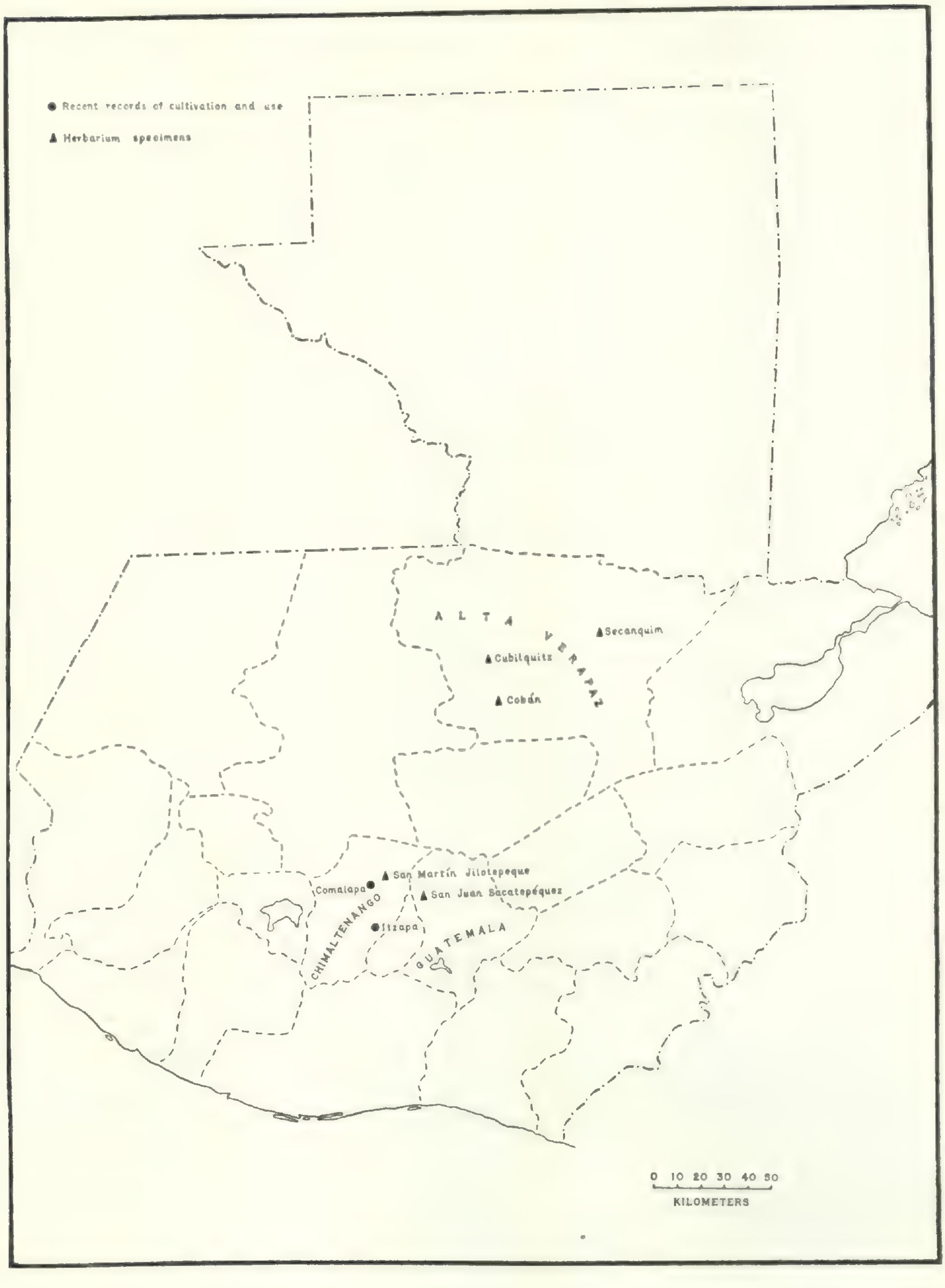

Fig. 2. Guatemala: Localities and regions where grain amaranth cultivation is indicated.

Wherever I saw the plants, I was told that the crop was much more important, grown in entire fields, among the uncivilized Indians far off in some vague areas of the back country. The plantings seen were on a very small scale and made by only a fraction of the people in each village. They said that they grew large quantities only as a catch crop when maize was scarce; usually a few plants were grown in the house lots or in the maize fields. The seeds are often sown in a new burning or in heavily manured ground and occasionally the plants are irrigated. Sometimes the plants were simply allowed to seed themselves from year to year. I talked to one Indian for quite a long time while he was chopping weeds and hilling his maize, and noticed that in several places he carefully avoided disturbing some volunteer amaranths.

The plants are generally called *bledo* in Spanish or some variant of *tez* in the Maya dialects. Varieties are distinguished on the basis of plant and seed color, but are not kept separate in cultivation.

The crop is planted at the start of the rainy season in April or May and is harvested gradually from September to January. Much of the seed is made into popped confections, bound together with brown sugar syrup, just like the *alegrías* of Mexico. In Guatemala, they are called *niguas*, the Spanish name for chiggers, perhaps because the seeds look like tiny insects (pl. 12B). The paler seeds pop better and are preferred for *nigua* making, although some black seeds are usually mixed in. Popping is done in small batches in the huts of the farmers, using the family *comal*. Sorghum seed is often popped by the same people to make a very similar confection called *alboroto*, and some hybrid confections include both amaranth and sorghum. During the drier season, when the cakes do not fall apart from the dampness, the people of San Martín Jilotepeque and San Juan Sacatepéquez peddle *niguas* and *alborotos* quite widely in the Antigua-Guatemala City area. Lots of the people who told me that no grain amaranths were grown in Guatemala had known about *niguas* all their lives, but they thought they were made from sorghum, like *alborotos*.

In Cobán cultivation is extremely inconspicuous and confections, called *jaleas*, are made only for home use. There the seeds are usually toasted and milled for *pinole*.

In San Martín Jilotepeque and San Juan Sacatepéquez, in addition to making *niguas*, the people prepare the seed in various ways for home consumption. Although they regard the seeds as healthful and nutritious, they seem to be rather apologetic about these practices; maize obviously has more prestige value. They make the seeds into a gruel or mill them for flour, which, with sugar added, is baked into bread. More commonly, however, they soak the seeds in hot water and grind them into dough for *tortillas*, alone or mixed with maize dough. White *bledo* seed is preferred for tortillas, but the black seeds are commonly used, since they are not acceptable for anything else.

PERU AND BOLIVIA

Records of grain amaranths in European herbals are of little value in the case of the North American races; they cannot be recognized in European botanical literature until centuries after the Conquest (Thellung, 1914, p. 236). In contrast, one of the South American grain amaranths, eventually named *Amaranthus caudatus* by Linnaeus, entered Europe very early as an ornamental plant. It can be traced through various late 16th century herbals (Thellung, 1914, p. 232), usually with no place of origin specified, until Clusius assigned it to Peru. Clusius apparently obtained some sort of evidence that the species was a South American grain crop; he presents a good illustration of the plant labelled "*Quinua, sive Blitum majus Peruanum*" (1601, Lib. 4:81). Clusius assumed that this was the same crop as the *quinoa* found in Ecuador by Pedro Cieza de León, which was undoubtedly a chenopod. This confusion is natural, since the name *quinoa* has often been used ambiguously for grain chenopods and amaranths and is still applied to both in parts of South America today. Linnaeus (1737, p. 443) cited Clusius in describing the same species and agreed that it came from South America.

In contrast to Mexico, the historical record of grain amaranths in the Andes is extremely poor. One reason may be that in western South America the activities and settlements of the Spanish colonists were concentrated on the coast, rather than in the highlands to which grain amaranths are almost invariably confined. Also, in the Andes grain amaranths may always have been a minor and localized crop, easily overlooked or confused with the similar and much more abundant grain chenopods.

The tremendous ceremonial role played by *huauhtli* in the Aztec Empire was taken over by maize in the Inca Empire. The Inca Feast of the Sun was in some ways startlingly like the Aztec feast of Huitzilopochtli. It too was the greatest feast of the year, held in the capital city with bloody sacrifices and colorful processions of all the chiefs and dignitaries. Just as in Mexico, the temple maidens on the night before the feast prepared a sacred bread, to be distributed and eaten ceremonially, but in Cuzco the bread was of maize (Means, 1931, pp. 368–372).

Thanks to the Jesuit chronicler Cobo (1653), there is one record of grain amaranths in colonial Peru. He distinguished *bledos* from *quinoa* and wrote that red and white *bledos* were "very common food of the Indians, and in the city of Guamanga (fig. 3) very pleasing candies are made of the seed of the white *bledos* and sugar" (See Appendix—I).

Until the present century no further notice of this crop seems to have been taken by anyone but the Indians. Finally Thellung (1914, p. 233) published a report by Spegazzini that the Chiriguano Indians around Tarija in Bolivia cultivated a white-seeded amaranth under the name of *Inca-pachaqui*, or Inca grain; they ate the seeds as meal or grits. In 1915 O. F. Cook collected a pale-seeded amaranth, called *quihuicha*, in the Urubamba Valley of Peru near Ollantaytambo. Cook later wrote that *quihuicha* was grown as a seed crop in the temperate valleys around Ollantaytambo and that the seeds popped like Indian corn (1925, p. 36).

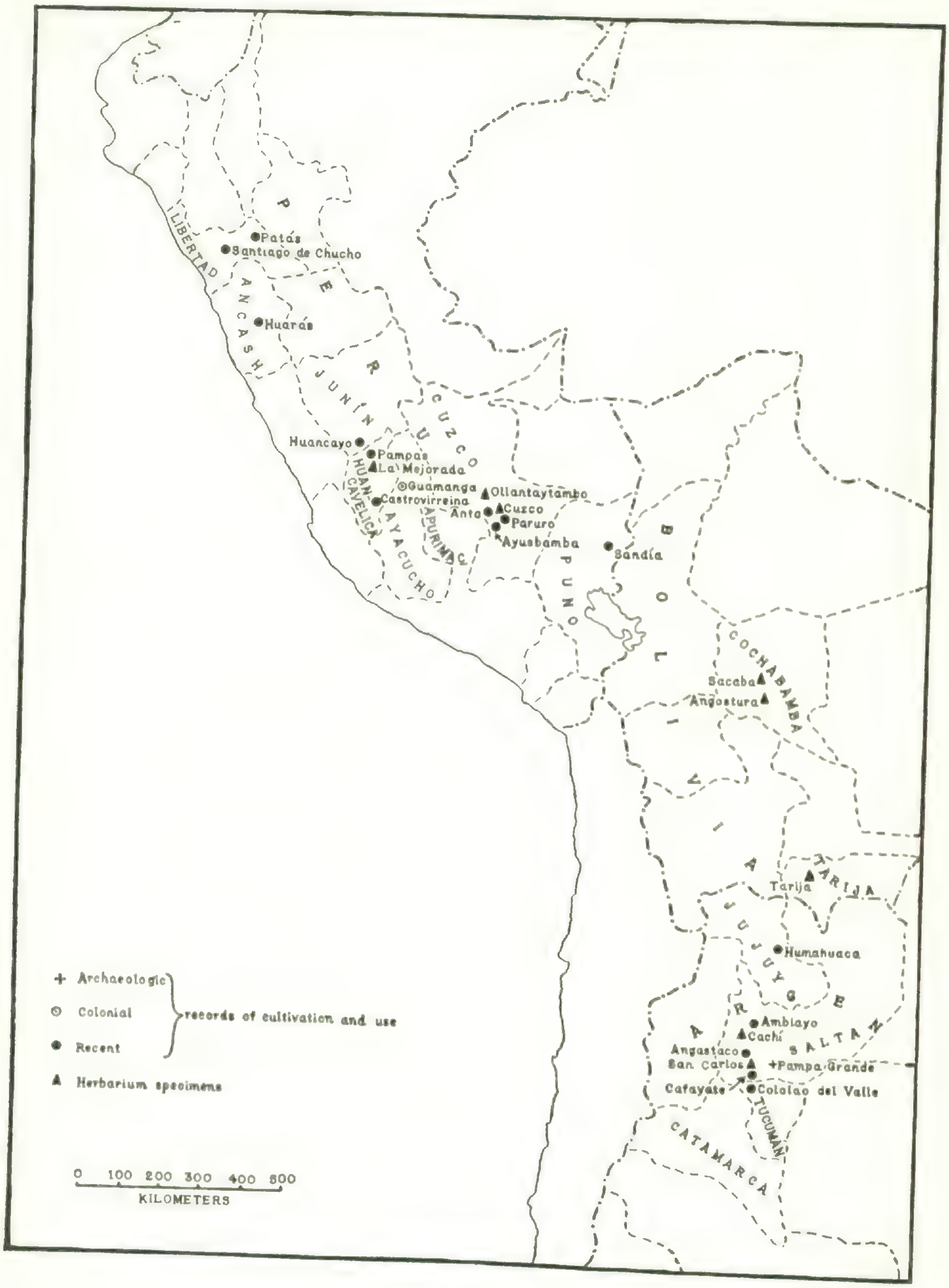

Fig. 3. South America: Localities and regions where grain amaranth cultivation is indicated.

At about the same time, Weberbauer found the plants growing near the Indian houses quite widely through the department of Cuzco (Herrera, 1921, p. 74).

In recent years the crop has been observed by botanists in various parts of Peru and Bolivia. In Peru it is reported at Patás and Santiago de Chucho in Libertad, at Huarás and the Callejon de Huaylas in Ancash, at Huancayo in Junín, at Castrovirreina, Pampas, and La Mejorada in Huancavelica, at unspecified places in Ayacucho and Apurimac, at Anta, Paruro, and Ayusbamba in Cuzco, and at Sandía in Puno (Herrera, 1940, p. 229; Hunziker, 1943b, pp. 338–339; Weberbauer, 1945, p. 619; Pulgar Vidal, 1946, 1:115; Arévalo, Cárdenas, and Rick, letters). In Bolivia the crop has recently been reported in Tarija where it was first found by Spegazzini, and also in the department of Cochabamba (Hunziker, 1943b, pp. 337–339). Cárdenas and Cutler have supplied me with seed collections from Sacaba and Angostura in Cochabamba.

Herrera believed the plant was an important ancient, possibly pre-Inca crop of the temperate valleys of Peru, which has declined to a relic in recent times (1940, p. 229). Pulgar Vidal (1946, 1:115) reported that it was an ancient widespread crop of the highlands, "but it is unknown in the city markets, its consumption being limited to the small harvests that each person obtains from the fringes of the maize fields." Other persons who have seen the crop in Peru agree that it is grown only by the Indians in small plantings on the edges of the maize fields (Weberbauer, 1945, p. 619; Rick, letter).

Cárdenas gives a similar picture for Bolivia. He wrote me that the grain amaranth "is becoming a very rare and odd foodstuff", and later (1949, p. 115) described it as an "autochthonous cultivated species on the road to extinction." As in Peru, the plants are not grown in pure stands, but are sown along the edges of the maize fields.

Both the Peruvian and Bolivian plants used for grain are mostly pale-seeded, but some dark seeds are usually mixed in. The seeds are prepared by toasting, parching, or popping; they are commonly eaten alone, sometimes in milk or in stews or mixed with other flour (Pulgar Vidal, 1946, 1:115; Arévalo, Cárdenas, Rick, letters).

The name *quihuicha* seems to be used only in the Cuzco area. Elsewhere in Peru the plants are called *achis, achita, ckoito, coyo,* or *coimi;* in Bolivia they are called *coimi, cuime, millmi* or *quinua millmi* (Cook, 1925, p. 99; Herrera, 1940, p. 229; Hunziker, 1943b, pp. 331–339; Weberbauer, 1945, p. 619; Pulgar Vidal, 1946, 1:115; Cárdenas and Hawkes, 1948, p. 31; Arévalo, Cárdenas, letters). In both countries, weed amaranths are given a different name than the grain crop, usually some variant of *jataco.*

ARGENTINA

In an archaeologic site, believed to be pre-Columbian, at Pampa Grande in the Argentine province of Salta, a funerary urn full of seeds was recently unearthed. Mixed in with maize, bean, and chenopod seeds were a quantity of

amaranth flowers and pale seeds, identified as *A. caudatus* by Hunziker (1943a). Since this species is unknown in a wild state, this discovery is good evidence that the crop is ancient in the northwestern Argentine.

Cultivation seems to have continued unnoticed by the outside world for many centuries. Finally, in 1897, Spegazzini visited the small Indian village of Amblayo in the mountains of Salta province and was "presented with some excellent little cakes which they said were prepared with Inca wheat of the locality." He took home some of the yellowish seeds and planted them; they grew into amaranth plants different from any known species, which he named *A. edulis* (Spegazzini, 1917, p. 163). Since then *A. edulis* and the Andean *A. caudatus*, both often grown together, have been found repeatedly as grain crops in the four northwestern provinces of the Argentine: Jujuy, Salta, Tucumán, and Catamarca (see fig. 3). Hunziker (1943b, pp. 325–339) gives a detailed summary of previous Argentinian records together with much new information from his own collections. The plants are usually called *quinoa* or *chaclión*, but the Andean name *coimi* is also used in the Argentine province of Jujuy.

The plants are cultivated only in small quantities, often in the maize fields, and it has become rare to find even a few plants; "there is no doubt that the days of *A. edulis* are numbered and that in a little while longer its cultivation will have fallen into oblivion" (Hunziker, 1943b, pp. 328–329).

ASIA

Ancient History.—In later sections of this paper, we shall see that the Asiatic and American grain amaranths are very closely related and that there is reason to believe that the entire group must have been originally domesticated in America. The question of how long they have been grown in the Orient is therefore of considerable interest.

The crop is scattered so widely through Asia and is so firmly entrenched among remote peoples that it gives a powerful impression of great antiquity in the area. Many investigators, from De Candolle (1883, p. 357) and Hooker (1885, p. 718) down to Ames (1939, p. 39), Vavilov (Darlington and Janaki-Ammal, 1945, p. 14), and Merrill (1950, pp. 16–17), have concluded that the crop has certainly been cultivated in southern Asia from time immemorial and probably originated there.

Unfortunately, there is little direct evidence available on the early story of grain amaranths in this area, and it seems unlikely that there will ever be much more. The crop may always have been concentrated, as it is today, in inaccessible highlands, mostly unknown territory to the ancient Oriental writers and early European travellers. The best hope of finding early records would seem to be in India, where the crop is most widespread and important. So far as I know, no one has ever looked in the old Hindu writings for records of these plants.

The ancient Chinese botanical sources have been carefully examined by Bretschneider. It is hardly to be expected that grain amaranths would be recorded in

these sources, since one can search long and vainly for any mention of them in modern botanical literature on China. Only one definite account of the crop in modern China seems to have been published (Hu, 1948). Therefore it is startling to find that Bretschneider (1896, p. 405) presents what seems to be a clear reference to a grain amaranth in an ancient Chinese materia medica. This work, written about 950 A. D. for the Prince of Shu, modern Szechwan, lists six kinds of *hien*, a generic name for a group of related plants, mostly indigenous amaranths cultivated as pot-herbs. Among these were two whose seeds were used in medicine; one was called *jen* (man) *hien*, possibly because it grew tall and erect. We shall see that there is a modern record of grain amaranths from the same area which gives the same name.

Recent.—Since early in the 18th century the grain amaranth species have been collected repeatedly in many parts of Asia (Martyn, 1728, p. 6; Linnaeus, 1763, p. 1406; Miller, 1768, p. 17; Willdenow, 1798, pp. 29–37; and many later sources). However, since these species have become widespread as cultivated ornamentals and occasionally as pot-herbs, their presence does not necessarily indicate cultivation for grain. Many of the collectors noted simply that the plants were cultivated, and there is no way of knowing whether they had found a few ornamentals in an Englishman's flower garden or the staple food crop of the entire region. Such cryptic records are of little value for our present purposes, although they suggest that the grain crop may be grown much more widely than the more definite records prove.

The first European to take an interest in the Asiatic amaranths as a grain crop seems to have been Francis Buchanan-Hamilton. In the early 19th century he found the crop in two widely separated parts of India, the far south and the fringes of the Himalaya.

South India and Ceylon—Buchanan-Hamilton named the white-seeded south Indian grain amaranth *A. frumentaceus*. He discovered it "on the hills between the Mysore and Coimbatore countries, where the natives call it *kiery* and cultivate it for the seed, which they convert into flour and which forms a great part of their subsistence" (Roxburgh, 1832, p. 609). Later Wight (1843, p. 720) wrote of *A. frumentaceus:* "In Coimbatore, Salem, and Madura I have frequently met with large fields of it, often on very steep slopes. The seed ground into meal forms the principal food of the wild inhabitants of these hills." Sykes (1838, p. 241) may have been referring to the same plant and the same area when he listed, among the crops of the Deccan, an amaranth called *rajgeerah* whose seeds were harvested in December and eaten unmilled.

The crop has persisted in these hills into the present century. In 1912 the U. S. Department of Agriculture received seeds of a grain amaranth from the Mysore area (Safford, 1917, p. 297). Finally, Fisher (1921, p. 147) reported that on the Anaimalai Hills at elevations of 2,000 to 4,000 feet the hillmen cultivated a grain amaranth called *kira*.

There are vague reports, with no details given, of cultivation of amaranths in Ceylon for the grain, locally called *landesi* (Hooker, 1885, p. 718; Church, 1886, p. 107; Trimen, 1895, p. 396).

North India—Buchanan-Hamilton gave the name *Amaranthus Anardana* to the white-seeded plants he found cultivated in the fields of Nepal, Bhagalpore, and Cosala, modern Oudh (Wallich, 1828, No. 6903; Madden, 1858, p. 118; Haines, 1922, p. 1247). In his notes he also mentioned that one of the chief crops high in the hills of Kullu was a plant called *chuyá*, which he had not seen but believed to be a grain sorghum (Madden, 1858, p. 118). Madden believed that *chuyá* and *anardana* were one and the same thing, and that *anardana* was an incorrect rendering of *amardana*, as Buchanan-Hamilton once wrote it, meaning immortal grain. He had seen this tall crimson or yellow amaranth cultivated "all over the Himalaya" under various local names, including *ramdana*, grain of the god Rama. The names given this crop in different regions of the Himalaya are bewilderingly variable and will not be catalogued here; many, such as *báthu* and *sag*, are generic terms applied not only to grain amaranths but also to chenopods and the various indigenous amaranths used as pot-herbs.

Later records show that grain amaranths are scattered widely across northern India and the neighboring states. Occasionally they are grown in the plains regions as an irrigated crop during the dry winter monsoon (Watt, 1908, p. 63; Bamber, 1916, p. 314). Little precise information is available on distribution of the crop in the lowlands. Kashyap (1936, p. 205) reports them around Lahore in the Punjab. White-seeded specimens of species commonly grown for grain have been reported in cultivation at Manbhum, Singbhum, and Sambalpur (Haines, 1922, pp. 761–762), but the purpose for which they were grown was not stated. In these plains areas the crop seems to be grown only on a very small scale along field borders, and the grain has a minor use as one of the foods permitted Hindus on their fast days.

Behind the plains, in the foothills and mountains of the Himalaya system, amaranths become an important field crop and a conspicuous feature of the landscape. They have been recorded repeatedly along the whole length of the Himalaya from Kashmir to Bhutan. Important early collections of grain amaranth species were made in Baltistan, Hazara, Kashmir, and Ladak by the Schlagintweit Tibetan expedition of 1856. The available herbarium specimens bear no data on uses, but Thellung reported that one of their collections, at least, was known to come from plants cultivated for the seeds, which were ground into meal (1914, p. 243). Subsequently, cultivation of amaranths as grain crops has been reported in Kashmir, Chamba, Sirmur, especially around Simla, in Bashahr, Tehri, Garhwal, Kumaon, specifically in the Bhotiya and Almora regions, in the mountain tracts of Oudh and Bengal, and in Sikkim (Powell, 1868, p. 244; Watt, 1885, pp. 210–211; Church, 1886, p. 107; Duthie, 1893, p. 24; Lawrence, 1895, p. 338; Gammie, 1898, p. 184; Collett, 1902, p. 411; Bamber, 1916, p. 314; Pant, 1935, p. 46; 83; Millen, letter). Watt also reported the crop in the hills of Burma (1908,

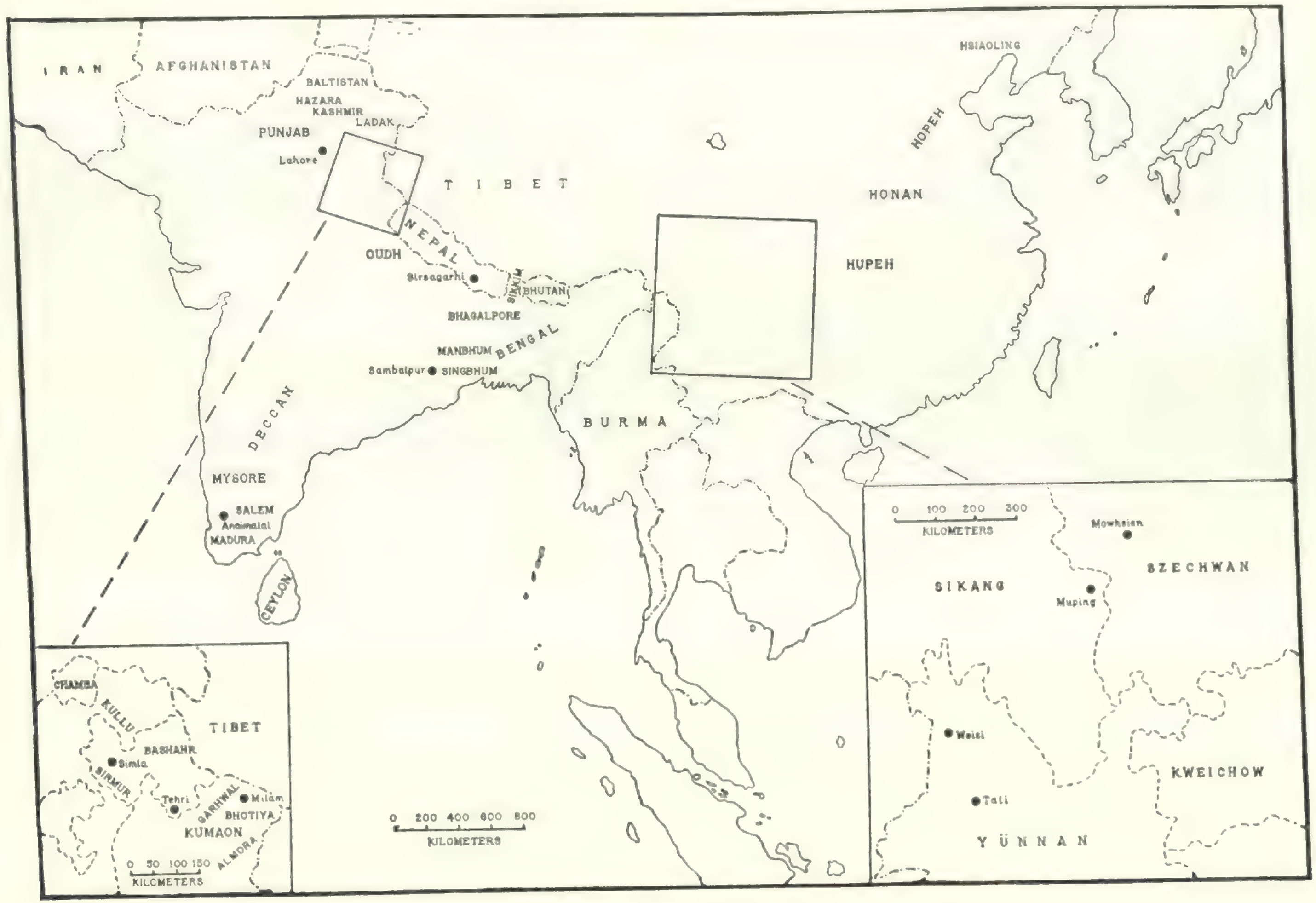

Fig. 4. Asia: Localities and regions where grain amaranth cultivation is indicated.

p. 63), but Stonor, who knows the area well, wrote me that he has never seen amaranths cultivated for grain in the Burma hills or the outer Himalayas of Assam. He has heard that they are grown as a grain crop on the Bhutan border by a Tibetanized tribe.

In Nepal there seems to have been no record of the crop since the time of Buchanan-Hamilton and Wallich until 1948, when Dr. Janaki-Ammal found amaranths cultivated as a grain crop near Sirsagarhi in the Marku Valley. She obtained samples of both pale- and dark-seeded kinds, which I have been able to grow.

Throughout the Himalaya, the crop is planted in unirrigated land at the beginning of the rainy summer monsoon in May or June and is harvested from September on (Watt, 1885, pp. 211–212; Church, 1886, p. 107; Duthie, 1893, pp. 23–24; Lawrence, 1895, p. 338; Watt, 1908, p. 63; Pant, 1935, p. 84; Millen, letter). The amaranth is a favorite crop in newly burned and cleared jungle, as it is not easily injured by wild pigs, bears, and deer (Watt, 1885, p. 211; Pant, 1935, p. 83). In the Valley of Kashmir, it is a relatively minor crop, as in the plains, sown in rows among the cotton fields or on the borders of the maize plots (Lawrence, 1895, p. 338). Around Tehri it is grown in little plots near the houses (Millen, letter). It is planted more extensively as a regular field crop higher in the Himalaya, often at elevations up to 2500 or 3000 meters (Hooker, 1885, p. 718; Watt, 1885, p. 211; Church, 1886, p. 107; also many later writers). Pant (1935, pp. 40–46, 84) gives a fascinating account of the precarious agriculture practiced by the Mongoloid nomads around Milam on the Tibetan frontier of Kumaon. The area is too high for permanent habitation. It is covered with six to twelve feet of snow for over half the year and the growing season is only about four months long. Crops are raised by primitive hoe cultivation in tiny steep plots studded with glacial boulders; the boulders aid growth of the plants by storing the sun's heat. The crops are always stunted, and often ruined by persistent mists or avalanches; sometimes they are buried by early snows before they can be harvested. In spite of these tribulations, the people sow and usually reap barley, buckwheat, and grain amaranths, sometimes at elevations of more than 3500 meters.

The Himalayan plants, like the Latin American ones, are rich and variable in color; their striking coloration is partly responsible for what little attention they have received in the available literature. Madden (1858, p. 118) was enthusiastic about the brilliant crimson and rich yellow of the plants: "The effect of a mountainside, terrace above terrace, covered with distinct fields of these colours, and glowing under the rays of the afternoon sun, is gorgeous indeed." Lawrence (1895, p. 338) described the amaranth as "the most beautiful of all the crops, with its gold, coral, and crimson stalks and flowers." Gammie (1898, p. 184) wrote that the amaranth, "with its ample red and yellow panicles, brightens the landscape, and its fields of vivid hue serve to mark the positions of widely scattered hamlets among the valleys, miles away from the traveller's standpoint."

Many of the writers give more space to the esthetics than to the uses of the crop, particularly since the grain does not enter into commerce. "Visitors to the hills of India are inclined to smile at people who live very largely upon these minute seeds" (Watt, 1908, p. 63). Around Tehri the grain is popped and made into a dough which is patted between the palms of the hands to make thin cakes (Millen, letter). In Nepal the grain is roasted and eaten as balls like popcorn, held together by sugar syrup (Janaki-Ammal, letter). There are a few reports that the seeds are parched, ground to flour, and eaten as a gruel with milk or water (Watt, 1885, p. 210; Lawrence, 1895, p. 338; Pant, 1935, p. 46). Beyond that there are only such general statements as: this grain is "one of the most important sources of food to the hill tribes of India" (Watt, 1885, p. 211).

Afghanistan and Persia—Referring to western Afghanistan and the Khorasan area of Persia, Atkinson (1891, p. 10) wrote:

> "The amaranth, *taj-kharus*, occurs only as a cultivated plant, usually seen thinly scattered through melon and tobacco fields, both the red and yellow flowered varieties. I never met with what I should consider a regular crop of the plant, but it occurred through fields rather as if the natives held, in superstitious veneration, the necessity of growing a few of these plants sparsely spread through their fields. The seed is eaten cooked."

China and Manchuria—Shiu-ying Hu (1948, pp. 32–34) wrote that an amaranth is cultivated in western China:

> ". . . . . as a supplementary crop in corn or cotton fields to fill in the spaces where young plants may have been destroyed by insects or along the margin of the field. The plant often grows to a man's height and is thus called manly *shien*. The crop is harvested when the leaves on the lower two thirds of the stem turn yellow. After the plants are gathered and dried in the sun, they are threshed."

The seeds are known as *tien-shu-tze*, or millet from heaven; they are popped and mixed with a hot sugar syrup made from fermented rice or millet grain. When the mixture cools, it is "cut into thin slices. This candy is crisp, puffy, sweet and well flavored. On the Chinese New Year's Eve, in every farm-house quantities of such candy are made." The Chinese characters on Miss Hu's illustration of manly *shien* are identical to those given for man *hien* in Szechwan in the 10th century (Bretschneider, 1896, p. 405). Miss Hu did not specify the parts of western China in which the crop is grown, but she suggested that I write M. C. Chang at Chengtu for definite information. Chang informed me that grain amaranths are not grown near Chengtu but in far-off mountain areas. He sent me samples of light- and dark-seeded *tien-shu-tze*, grown at elevations of 2000 or 2500 meters near Mowhsien in northwestern Szechwan and Muping in Sikang.

The crop is probably also present to the southwest of Szechwan in Yünnan; amaranths are reported extensively cultivated on the upper Mekong above Weisi and also around Tali (Handel-Mazzetti, 1929, 7:162). The fields are said to "appear generally red" from these plants. Although no mention of use is made, it is hard to imagine such large-scale cultivation as anything but a grain crop. It is conceivable that the crop may extend almost continuously through these poorly known parts of interior Asia from Szechwan to the Himalaya.

On the other side of Szechwan, the trail is not much clearer. Pale-seeded forms of species ordinarily grown for grain have been collected in cultivation in Kweichow and Hupeh, but with no data on use. Small-scale cultivation of amaranths for their edible seeds has been noted in Honan and Hopeh (Hsien-wu, 1935, p. 11; Beach, letter), but no details are available.

These indistinct traces of the crop, extending across so much of the interior of China, finally come to an end in Manchuria. A pale-seeded cultivated amaranth belonging to a grain species was collected in the Hsiaoling area of southern Manchuria by Dorsett in 1925. In northern Manchuria there is a definite account of grain amaranth cultivation (Skvortzow, 1926, p. 15). The crop "is planted in fields by the Chinese for the sake of its small yellow or reddish seeds, which are used in the preparation of little cakes."

AFRICA

Baker and Clarke (1909, p. 32) claim that amaranths are "cultivated throughout warm Africa as a grain." This statement may be an exaggeration based partly on simple records of occurrence of grain amaranth species. In Africa, just as in Asia, some of these species have been widely diffused as garden ornamentals; occasionally they are also cultivated as pot-herbs. I am unable to find any confirmation of grain use of the plants in Africa, except for Dalziel's statement that in Sierra Leone an introduced amaranth "is said to be cultivated for the seed as food" (1948, p. 36).

II. BOTANICAL CLASSIFICATION

So far, in tracing the culture history of the grain amaranths, the problem of their botanical classification has been postponed and species identifications given in the literature have been deliberately ignored. The Latin names given the plants by different authors are bewilderingly variable. They include, for the grain amaranths of Arizona: *caudatus, leucospermus, leucocarpus, Powellii,* and *retroflexus;* for those of Mexico: *caudatus, cruentus, hybridus, leucocarpus, leucospermus,* and *paniculatus;* for those of South America: *caudatus, edulis,* and *leucospermus;* for those of Asia: *Anardana, caudatus, celosioides, cruentus, farinaceus, flavus, frumentaceus, hybridus, hypochondriacus, paniculatus, sanguineus, speciosus,* and *strictus;* and for those of Africa: *Alopecurus* and *caudatus.* Conflicting identifications are not confined to older sources but continue in recent literature and current herbarium determinations.

A little investigation of the published descriptions of these many "species" immediately reveals one important fact: all belong to a closely related group, forming a relatively small section of the genus *Amaranthus.* This section, usually called AMARANTHOTYPUS, is distinguished by having monoecious compound inflorescences and 5-merous flowers with circumscissile utricles (Dumortier, 1827, p. 19; Moquin-Tandon, 1849, p. 255; Thellung, 1914, p. 230). Beyond this single fact, very little sense can be made of the classification of the grain amaranths from a study of the literature. The section AMARANTHOTYPUS is outstanding, even in

the genus *Amaranthus*, for its labyrinth of disputed synonymy and controversial taxonomy.

The confusion is mostly traceable to two factors: the wide dispersal of the species and the subtlety of the differences between them. Their wide distribution is not due solely to their spread as grain crops; the grain species and their close relatives include most of the cosmopolitan ornamental and weed amaranths. Since there has been nothing approaching an adequate general treatment of the genus until the present century, the naming of amaranths has been almost entirely in the hands of persons working on local floras. It was inevitable that such widespread species would receive different Latin names in different regions. The result has been a rich heritage of problems in nomenclature.

The second factor responsible for the confused classification has created a much more serious problem than the superfluous names. Species differences within the section are mostly quantitative and often easier to recognize than describe. Most of the earlier species descriptions are excessively brief and waste their few words on characters common to many species or such trivial characters as pigmentation. Before the extreme importance of flower characters was realized, the damage had been done. The species had been described and named, according to the rules, but many were completely unrecognizable from the original descriptions. Since access to many of the type specimens has been difficult or impossible for most botanists, it is small wonder that concepts of the species have become highly variable.

The obvious solution to these difficulties would be monographic treatment, a formidable project which no one has yet attempted. The closest approach was made by Thellung in his treatment of *Amaranthus* for a flora of Europe (1914). Thellung's work is an admirable piece of scholarship, based on careful herbarium study, emphasizing microscopic flower characters, and on exhaustive bibliographic research. Unfortunately, the purpose of the work required Thellung to concentrate his attention on the European flora, which has few native amaranth species. He concluded that all the species of AMARANTHOTYPUS present in Europe are recent immigrants, none of which arrived before the 16th century. The specimens he worked with consisted mostly of adventive weeds and a jumble of cultivated plants, often hybridized and usually of forgotten origin, which had been propagated for generations in European gardens. Considering these fantastic handicaps, Thellung's insight into the group was remarkable. His reduction of over forty "species" of AMARANTHOTYPUS to five and his detailed descriptions of the entities, often based on re-examination of Linnaean types, represent great forward steps.

There have been two important taxonomic works involving this group since Thellung's work. Standley's treatment of the genus for the 'North American Flora' (1917) is particularly useful for the North American endemic species; his systematic treatment of the section AMARANTHOTYPUS is little more than a simplification and modification of Thellung's treatment. Hunziker's morphological investigation of the grain amaranths (1943b), is also of considerable value, particularly for the South American crop plants, on which most of his work was done.

The best hope for fuller understanding and more convincing classification would seem to lie in a study of the entire section throughout its range. A start on this ambitious project is attempted here.

METHOD OF INVESTIGATION

The procedure adopted was to put aside all the conflicting identifications, both in published literature and on herbarium sheets, and make a fresh start by re-examining individual specimens. Specimens of the cultivated grain amaranths were mostly obtained by growing seed collections from many different sources in the New and Old World. Half a dozen to a dozen plants were grown from each seed sample in various greenhouse and outdoor plantings, both in Missouri and in California. I was able to make some field collections of non-cultivated amaranths in the United States, Mexico, and Guatemala. However, most of the wild and weed amaranths examined, as well as a few of the grain amaranths, were obtained from the collections of four herbaria: the U. S. National Herbarium, the Gray Herbarium, the University of California Herbarium, and the Herbarium of the Missouri Botanical Garden. Material examined from these institutions included their complete collections of the section AMARANTHOTYPUS from Latin America, Asia, and Africa, and a sampling of their collections from the United States. The specimens examined are listed on pages 620–623. A limited amount of material from Europe was examined, but is not included in the presentation, since the grain species and their close relatives are present in Europe only as recent immigrants.

I had originally hoped that chromosome counts might be of some help in classification. The few published counts indicate that there are two groups of species in the section AMARANTHOTYPUS, one with a diploid chromosome number of 32, the other with 34 (Takagi, 1933, p. 556; Murray, 1938, p. 317). I prepared root-tip sections of several species and obtained counts in the low 30's for all of them. In my preparations it was very difficult to obtain precise counts; the apparent number of chromosomes varied considerably between different cells of a single section. I suspect that other persons have had the same difficulty. For example, Takagi reported a diploid number of 32 for *A. caudatus;* in 1948 Dr. Cárdenas wrote me that he had found the diploid number in both *A. caudatus* and its wild relatives in Bolivia to be 32, but in a later publication (Cárdenas, 1949, p. 114) he reported counts of 34 for these same species. I am not convinced that the reported variations in chromosome number actually exist. In any case, the numbers are too difficult to determine in this group to be of much use in classification. It seemed best to rely entirely on morphological characters, at least in this preliminary attempt at classification.

Major attention was given to the morphology of the flowers, which were examined under a low-power dissecting microscope. There is always much variation between flowers on an individual plant, so that characterization by examination of one or a few flowers is unsafe. When a sufficiently large number of flowers is examined, a single reasonably constant type can be distinguished, which appears over and over again among the many other inconstant and non-repeating variants.

The abundance of flowers on an individual amaranth is one of the few consolations in studying this generally unattractive plant.

Mature flowers of each specimen were scored for about two dozen different items, involving number, size, and shape of all parts. Exact scale drawings were made of all specimens that appeared even slightly different from ones previously drawn. By means of such sketches several characters which have not received much previous attention are seen to be of distinct diagnostic value (see figs. 5 and 6).

An attempt was made to score macroscopic characters, particularly configuration of the inflorescence, but these proved to be of little value in classification. Such characters are difficult to measure or express objectively and are extremely dependent on the age of the plant and on environmental variables.

When examination and scoring were completed, it was found that the great majority of the available specimens could readily be sorted, on the basis of flower characters alone, into a few reasonably homogeneous groups. It then became evident that the vague and largely subjectively appreciable differences in vegetative characters and inflorescence aspect fitted these groupings quite well.

Finally, an attempt was made to determine the correct names for the major entities recognized; no attempt was made to give Latin names to the lesser entities. Where type specimens are not available, I have tried to do the least possible violence to existing species concepts, particularly those of Thellung and Standley. Standley's numerous herbarium determinations are outstanding for their consistency among the ruck of carelessly given names.

The following sections outline the distributions and the more distinctive characteristics of the entities recognized. Unless otherwise stated, the geographic distributions are based entirely on specimens examined. The grain species are considered first, followed by the closely related wild and weed species.

GRAIN SPECIES

The cultivated grain amaranth species are so very much alike, not only in appearance but in many technical characters, that the prevailing confusion is not at all surprising. All are coarse annual herbs with similar leaves and branching habit, erect and tall, sometimes growing higher than a man. The obvious plant and seed color differences, which have been used as varietal or even specific characters by too many botanists, are of little taxonomic value. *Amaranthus edulis* plants apparently always lack red pigment and are always pale-seeded, but each of the other three species has dark- and pale-seeded forms, and in plant color each varies from deep red to bright green. These color characters seem to be freely exchanged within an otherwise homogeneous population and are commonly highly variable in a single seed lot.

All the grain amaranths characteristically have great compound inflorescences, terminal on the main stem and side branches. The basic units of the inflorescence are little dichasial cymes, usually called glomerules, each ordinarily consisting of an initial staminate flower and an indefinite number of pistillate flowers. The

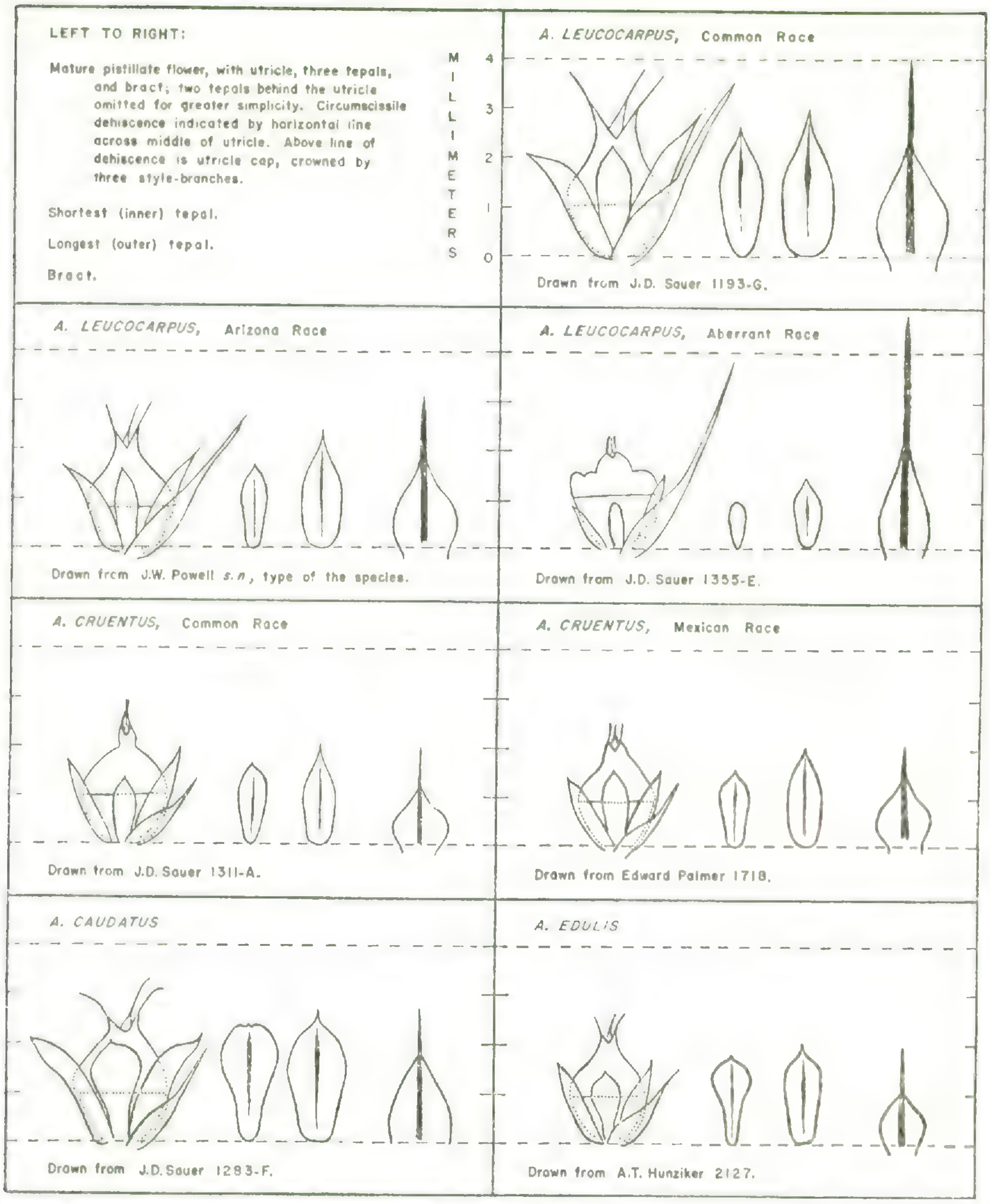

Fig. 5. Grain amaranth species. Scale drawings of pistillate flowers.

glomerules are crowded on a leafless axis to form complex inflorescences, technically thyrses, which are generally called spikes. When grown under unfavorable day-length conditions, the plants begin to bloom when only a couple of inches high and manage to produce only a simple small terminal spike. When grown under proper day-length conditions, all of the grain species are capable of putting forth a huge inflorescence, with a large terminal spike and fifty or a hundred lateral spikes, which may themselves bear branch spikes.

In all the grain species each flower is subtended by a sharp-pointed bract (fig. 5); the perianth consists of five free tepals; the male flowers characteristically have

five stamens, the female a single circumscissile utricle. Within this common framework, the following entities can be recognized.

Amaranthus leucocarpus S. Wats.—

This species was originally described by Watson (1875, p. 347) on the basis of plants grown from a single seed lot, obtained in Arizona by J. W. Powell. So far as I know, the species has not subsequently been collected in Arizona, but very similar plants have been widely collected elsewhere, particularly in Mexico. As defined here, the species is divided into races, with the type collection of the speciés assigned to the Arizona race. The more common and widespread race differs slightly from Watson's type, but includes Mexican specimens identified as *A. leucocarpus* by Watson himself (1887, p. 446). The species name was poorly chosen, since it was the color of the seeds, rather than the color of the fruit, which attracted Watson's attention. He later (1887, p. 446) attempted to change the name to *A. leucospermus*, but under the rules this later synonym is illegitimate.

In published works, *A. leucocarpus* is commonly reduced to a variety or synonym of either *A. caudatus* L. or *A. hybridus* L. Herbarium specimens of this group are commonly identified as either *A. paniculatus* L. or *A. hypochondriacus* L. There are morphological and geographical arguments against identifying the group which includes Watson's type with any of these Linnaean names. However, it is quite possible that *A. leucocarpus* may eventually prove to be a synonym of some other early name. For example, Wight's illustration (1843, p. 720) of *A. frumentaceus* Buchanan-Hamilton suggests that this poorly known species may be identical to *A. leucocarpus*. In the meantime, it is expedient to retain Watson's epithet, as it is the only one in common use which can definitely be tied to this distinctive group of amaranths.

Common Race of A. leucocarpus.—This race is perhaps more widespread and important as a grain crop than any other amaranth and also includes one of the common ornamental forms, sometimes known as Prince's Feather.

As a grain crop its known distribution includes many places in Mexico: Guasaremos and Rancho Trigo in Chihuahua (see fig. 1), Quebrada de Manzana in Sinaloa, Guadalajara and Tlajomulco in Jalisco, Teremendo and Opopeo in Michoacán, San Gregorio Atlapulco and nearby villages in the Distrito Federal, Amaxac and San Miguel del Milagro in Tlaxcala, Teocuizmanalco in Puebla, Chilapa in Guerrero, and Ixtlán de Juárez in Oaxaca. The specimen from Secanquim in Guatemala, previously mentioned as probably representing a grain crop, also belongs to this race. In Asia the race has been collected in Iran and Afghanistan; in many regions of the Himalaya: Baltistan, Hazora, Kashmir, Ladak, Chamba, Bashahr, Sirmur, Garhwal, Kumaon (labelled *A. Anardana*), Nepal, and Sikkim; in various provinces of China: Sikang, Yünnan, Kweichow, Szechwan, Hupeh, Kiangsu, and Shantung; and in Manchuria. Many of these Asiatic specimens bear the simple notation "cultivated" or "crop" but almost none are accompanied by any information on the purpose for which they are grown. Only the specimens grown from seed collected for me in Nepal by Dr. Janaki-Ammal are positively

identified as a grain crop. However, the distribution pattern of this race in Asia coincides strikingly well with the area of grain amaranth cultivation reported in the literature.

As an ornamental the race is widely grown in Europe and the United States. The only available African specimen is from Morocco and may represent an ornamental brought from Europe.

Outside of cultivation, the race has been collected only as an infrequent escape at widely scattered places in the United States, Mexico, Asia, and Europe.

The mature inflorescences of this race are remarkable among the cultivated amaranths for their stiff appearance (pl. 13A). Both terminal and lateral spikes are usually long and thick and often erect. The bracts are especially large and long-pointed, giving the inflorescence a prickly appearance. The tepals also are longer than in the other grain amaranths, slightly recurved, and usually acute-tipped (fig. 5). The utricle cap is large and slopes gradually to the extremely thick bases of the recurved style-branches, which usually meet in a sharp cleft. The Mexican populations are overwhelmingly pale-seeded, although several have a small proportion of dark-seeded forms mixed in. In the Asiatic collections dark-seeded plants are more numerous but still in the minority. The plants grown as ornamentals in Europe and the United States seem to be invariably dark-seeded.

There is minor but definite variation in flower characters within and between many of the Mexican collections. Some members of the Oaxaca and Guerrero collections show some resemblances to the Mexican race of *A. cruentus*, described below. All of the United States and Old World collections examined are virtually identical in flower characters and are exactly like some of the Mexican plants.

Arizona Race of A. leucocarpus.—This race is known only from the single 19th-century seed collection from some mysterious Arizona Indian tribe. All the available specimens were grown at the botanical garden of Harvard University. The vegetative characters and inflorescence aspect (pl. 13B) of the plants were probably marked by this exotic environment. The less plastic flower characters are very similar to those of the preceding race, except that the parts are all noticeably smaller and the style-branches less thick (fig. 5). The three available specimens are all pale-seeded.

Aberrant Race of A. leucocarpus.—One of the Mexican grain amaranths is quite unlike any recognized species. It seems best not to give it a Latin name until it is more adequately collected and understood. It is placed here provisionally, since it is grown within the range of *A. leucocarpus* and may be nothing more than a cross between it and some other very dissimilar species. This race is known only from Dr. West's collection from Los Reyes in Michoacán, where it is cultivated as a grain crop.

The inflorescences (pl. 13C) are much like those of the common race of *A. leucocarpus*, but the flowers are completely different. The stamen and tepal numbers vary between 4 and 5 in an individual inflorescence. The bracts have a narrow lamina and an extremely long point, while the tepals are greatly reduced in size

and often without visible nerves. The utricle cap is very rugose and flattened and the style-branches are extremely short.

There is only minor variation between the half dozen plants of West's seed collection that I have grown. All are dark-seeded.

Amaranthus cruentus L.—

Linnaeus described this species from Chinese plants (1759, 2:1269). His ambiguous description was clarified by Thellung (1914, p. 243) after re-examination of Linnaeus' material. There can be little doubt that the species under consideration here is the same as Linnaeus' *A. cruentus*. The plants included here which were determined by Standley are consistently labelled *A. cruentus*. Nevertheless, other taxonomists have given this species a variety of other names in herbaria; many of the Asiatic specimens have been labelled *A. paniculatus* L., a name reduced to synonymy with *A. cruentus* by Thellung and Standley.

Common Race of A. cruentus.—This group is known as a grain crop only at three places in Guatemala: San Martín Jilotepeque, San Juan Sacatepéquez, and Cobán. The specimen previously mentioned as collected in a maize field at Cubilquitz, which may have been grown for grain, also belongs here.

As an ornamental the race is cultivated over much of the world and is occasionally collected as an escape at widely-scattered places. Specimens have been examined from a few places in the United States all the way from Massachusetts and South Carolina to California; the states of Puebla, Vera Cruz, and Oaxaca in Mexico; British Honduras, Guatemala, El Salvador, Nicaragua, Panama, Porto Rico, Haiti, the Dominican Republic, Barbados; the departments of Atlantico, Antióquia, Cauca, and Cundinamarca in Colombia; Ecuador; Mérida in Venezuela; the states of Pernambuco, Minas Geraes, and São Paulo in Brazil; Hawaii, the Fiji Islands, New Guinea, Sumatra, British North Borneo; the islands of Mindanao, Mindoro, and Luzon in the Philippines; Japan; the provinces of Kiangsu, Anhwei, and Chekiang in China; Annam in Indo-China; Kenya and Uganda in British East Africa; and Coquilhatville in the Belgian Congo.

The inflorescences of this race are much more lax and usually more slender than those of *A. leucocarpus* (see pl. 13D). Though the slender bract points extend well beyond the laminas, the bracts are very small, so that the inflorescence has a soft appearance. The tepals are characteristically much shorter and slightly less acute than in *A. leucocarpus* and they are not recurved. The utricle cap is unique among all the amaranth species I have seen, being contracted into a narrow tower below the bases of the style-branches; the style-branches are slender and erect.

Except for some variation in tepal length, most noticeable in the Central American specimens, this race is very homogeneous. The Guatemalan grain specimens are both pale- and dark-seeded, in about equal proportions. All the other specimens are dark-seeded.

Mexican Race of A. cruentus.—This group has a curiously scattered distribution in Mexico: Acatlán in Puebla, Zimatlán in Oaxaca, Ymala in Sinaloa, and

Cusihuiriáchic in Chihuahua. It is known to be a cultivated grain crop at all these places except Cusihuiriáchic, where it was collected without data. An amaranth very closely related to this group is cultivated by the Pueblo peoples of the southwestern United States as a dye plant (J. Sauer, in press).

In inflorescence (pl. 14A) and most flower characters this race is very close to the common race of *A. cruentus*. It differs mainly in the shape of the utricle cap, which appears to be intermediate between *A. cruentus* and *A. leucocarpus* or *A. hybridus*. All the grain specimens are pale-seeded; the specimen from Cusihuiriáchic and the Pueblo dye plants are dark-seeded.

Amaranthus caudatus L.—

As mentioned in the discussion of grain amaranth cultivation in South America, this species was originally described from Peru. Thanks to the strikingly long and drooping tail-like inflorescence, which gives the species its name, the species has been more consistently recognized than most of the others. Nevertheless, specimens of *A. caudatus* are often mislabelled in herbaria, and at least one later synonym, *A. Alopecurus*, is found in the literature. The name *A. Alopecurus* was given by Hochstetter to a group of specimens collected in Abyssinia, which he apparently believed represented an endemic African species. All the collections cited in the original description of *A. Alopecurus* (Braun and Bouché, 1872) have been examined and found to be indistinguishable from South American collections of *A. caudatus*.

This is the second of the great grain amaranth species; it is grown as a crop in both South America and the Old World. Specimens known to represent the grain crop are available from several Andean places: La Mejorada, Ollantaytambo, and Cuzco in Peru; Sacaba, Angostura, and Tarija in Bolivia; San Carlos in Argentina. As in the case of *A. leucocarpus*, most of the Old World specimens are marked as cultivated, but almost none are accompanied by any data on the reason for cultivation. Janaki-Ammal found *A. caudatus* grown for grain in Nepal, along with *A. leucocarpus*. The known distribution of the species in Asia is strikingly like that of *A. leucocarpus* and of the localities in published records of grain amaranths. Specimens are available from Afghanistan, Baltistan, Ladak, Kumaon, and Nepal in the Himalaya; Yünnan and Szechwan provinces in China; and Manchuria. The published records of grain amaranth cultivation in Africa identify the plants as *A. caudatus* or *A. Alopecurus*. The species has been collected not only in Abyssinia, where it is apparently ruderal, but also in the Sudan and the Belgian Congo. None of the available specimens bear any data on use of the plants.

The species includes the familiar ornamental Love-lies-bleeding, grown in many parts of the world and infrequently collected as an escape.

The inflorescences are quite distinctive in that they usually have an extremely long, thick, trailing terminal spike. The individual glomerules become quite large and are relatively far apart, giving the spikes a peculiar knobby appearance. The "tail" is most conspicuous in the ornamental forms, which commonly have only a few lateral spikes. Many of the South American grain specimens also have the

long "tail" with few lateral spikes (pl. 14B), but others have an inflorescence more like that of *A. cruentus*, with a relatively inconspicuous terminal spike and many lax lateral spikes.

The bracts are usually fairly short and the laminas have broader bases than in the preceding species. The tepals are very broad toward the tips, often overlapping, and are strongly recurved. Even the outer tepals are somewhat obovate and the inner are definitely spatulate with a narrow claw. The inner tepals are obtuse-tipped or even emarginate. The style-branches are recurved, as in *A. leucocarpus*, but they are usually less thick and meet in a saddle rather than a cleft. The South American grain specimens are predominantly pale-seeded, but there are some reddish-seeded and some dark-seeded plants in most of the collections. The other specimens are mostly reddish-seeded, but a few of the Asiatic and African specimens have dark seeds.

There is much minor variation in flower characters within this species, particularly in the South American collections. One plant collected at San Carlos in Argentina deserves special mention. It is known to be derived from a mixed population of *A. caudatus* and *A. edulis*, grown together as a grain crop. Its inflorescence is approximately like that of other specimens of *A. caudatus*, and it lacks the polymerous staminate flowers which supply the key character of *A. edulis*. However, the pistillate flowers are almost indistinguishable from those of *A. edulis*.

Amaranthus edulis Spegazzini.—

This species was described by Spegazzini (1917, p. 163) from grain amaranths discovered at Amblayo in the Argentine province of Salta. The species has subsequently been found, always as a pale-seeded grain crop, only at a few other places in Salta and the neighboring provinces of Tucumán and Jujuy (Hunziker, 1943b, p. 325). Specimens are available to me only from Cachí, San Carlos, and another unidentified locality in Salta province.

The inflorescence of this species is its most distinctive feature. Instead of the indeterminate thyrse common to the other species of AMARANTHOTYPUS, this species has inflorescence branches terminated by a peculiar 7- to 9-merous staminate flower. The non-terminal staminate flowers have the usual 5 parts. As a result of their determinate growth, the spikes become extraordinarily blunt and club-shaped (pl. 14C). In pistillate flower characters the species is not extremely different from *A. caudatus*. The tepals are smaller and less strongly recurved and the style-branches are erect. A specimen from the mixed population at San Carlos is especially similar to *A. caudatus*.

NON-CULTIVATED SPECIES

Several species belonging to the section AMARANTHOTYPUS are recognizable among the wild and weed specimens examined. These share with the grain species the characters of the section: monoecious compound terminal inflorescences, 5-merous flowers, and circumscissile fruits. The non-cultivated plants are characteristically much smaller than the grain plants and have smaller flowers and

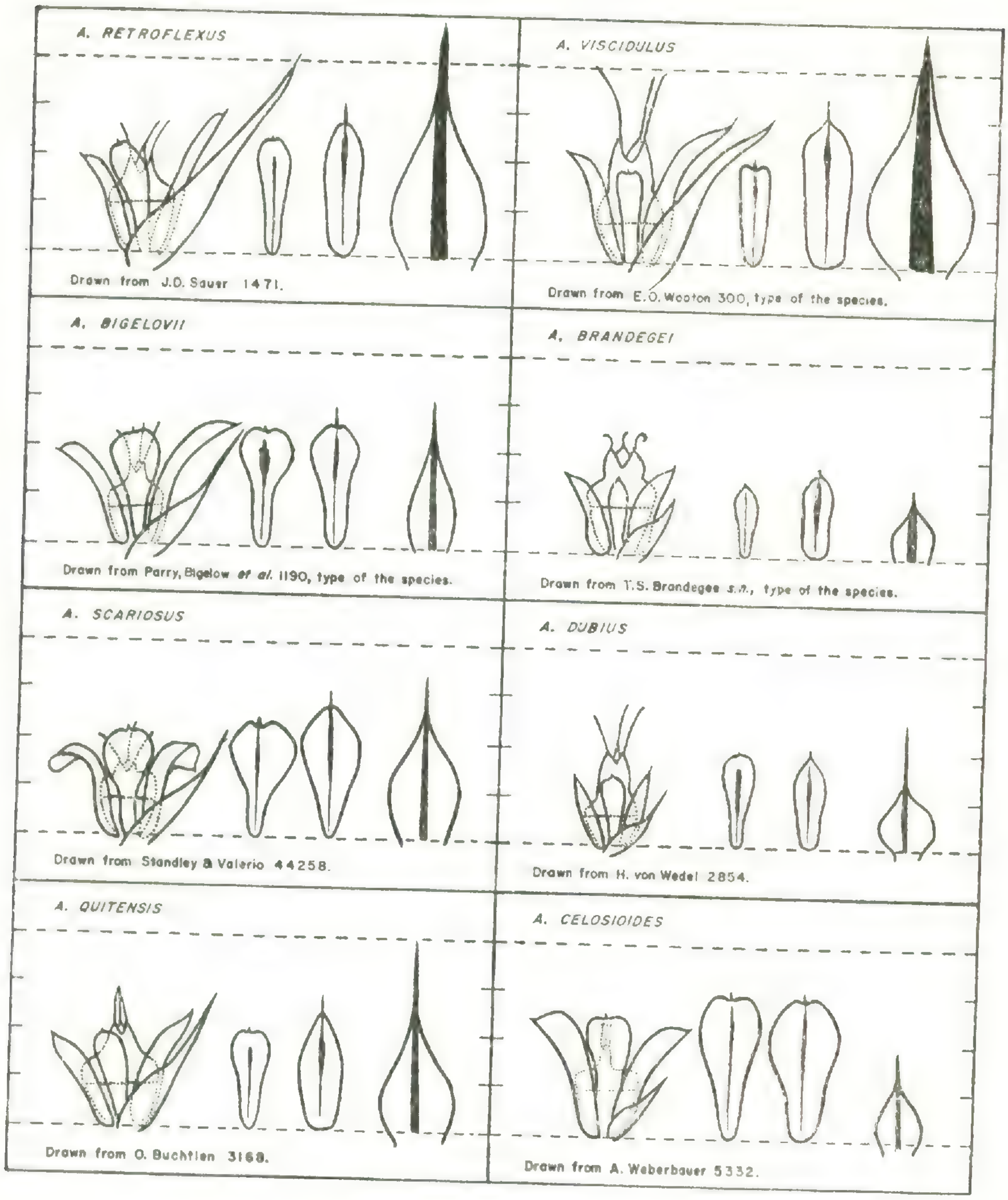

Fig. 6. Non-cultivated species of section AMARANTHOTYPUS. Scale drawings of pistillate flowers. (For explanation see fig. 5.)

fruits (fig. 6). They are invariably dark-seeded.

A distinction between weed species and truly wild species would be most desirable, but is not feasible since few of the available herbarium specimens bear adequate habitat data. Moreover, even in a field study such a distinction would be very difficult; throughout most of Latin America today, amaranths and other plants eaten by the ever-present livestock are difficult to find in natural habitats. Even the species which are not particularly weedy could be expected to be most abundant where they are protected by walls and fences.

The non-cultivated species are here arranged, as were the grain species, in rough geographic sequence from north to south, as they occur in the New World. Two

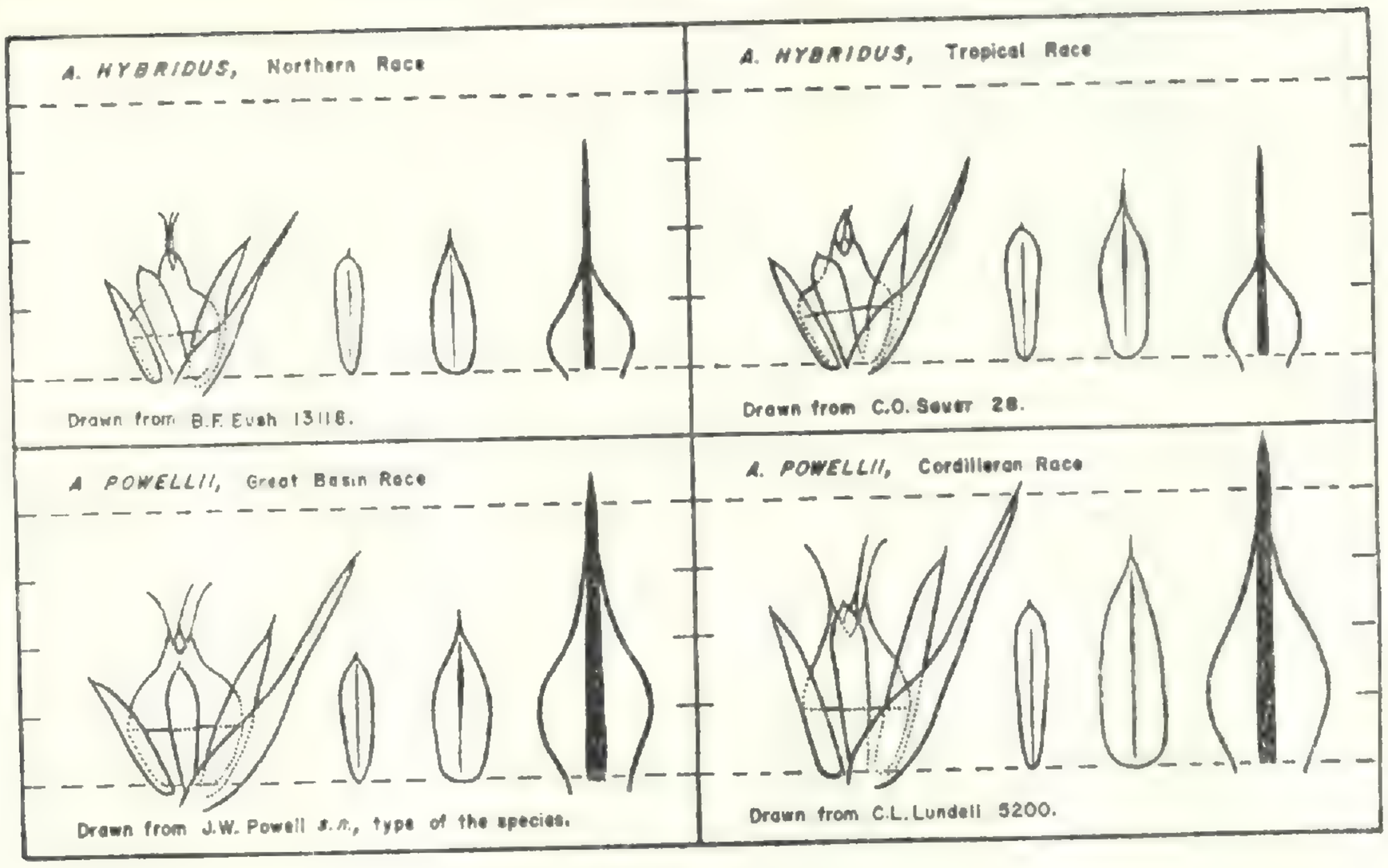

Fig. 6. Continued.

species, *A. hybridus* and *A. Powellii*, with a wide latitudinal range will be considered last. Another species, *A. spinosus*, which is usually included in this section of the genus, is not discussed here; it is a widespread tropical weed quite similar in many ways to *A. dubius* (see below), but not very similar to any of the grain species. It is readily distinguished from all the other species of the section not only by the peculiar spines but also by the anomalous arrangement of staminate and pistillate flowers in the inflorescence. The peculiar distribution of sexes in the inflorescence of *A. spinosus* is discussed in detail by Murray (1940a).

Amaranthus retroflexus L.—

Linnaeus gave the home of this species as Pennsylvania (1753, 2:991); his specimens were grown in pots from seeds collected by Peter Kalm. The name was suggested by a "deformed example with backward-bent branches" (Thellung, 1914, p. 254). The original description was ambiguous, but has been amplified by Thellung and others. There is fairly good agreement as to the nature of the species, both in the literature and in herbarium determinations, although confusion with other species, particularly *A. hybridus*, is by no means unusual.

This is one of the most abundant and widespread of the North American weed amaranths. It has been collected, almost invariably in disturbed habitats, over most of the United States and at scattered places elsewhere. Specimens are available from: Ontario, New Hampshire, Massachusetts, Connecticut, New York, New Jersey, Pennsylvania, the District of Columbia, West Virginia, South Carolina, Florida, Louisiana, Michigan, Indiana, Illinois, Minnesota, Iowa, Missouri; North and South Dakota, Nebraska, Kansas, Oklahoma, Texas, Montana, Colorado, New Mexico, Arizona, Idaho, Utah, Oregon, and California; also from Coahuila, Mexico; from Japan; from Hopeh and Shantung provinces in China; Kashmir in India;

Uzbekistan in the U.S.S.R.; Persia, Iraq, Armenia, Palestine, Algeria and Morocco. Thellung (1914, p. 254) cites numerous collections from Europe.

The inflorescence of this species is extremely thick, stiff, and erect. The numerous lateral spikes are quite short and crowded together. (One small group of specimens from Coahuila, Mexico, is distinctive in having a small inflorescence without lateral spikes.) The bracts are large, with unusually heavy midribs; the points of the bracts, though not long-excurrent beyond the laminas, commonly extend well beyond the flowers and give the inflorescence a rough, bristly look.

The tepals are much longer than the fruit, usually definitely recurved near the tips, and obovate or slightly spatulate (fig. 6). The tepals are somewhat indurated at the bases in mature flowers. The inner tepals, and often the outer also, are definitely obtuse or emarginate at the tips. The style-branches are erect or slightly recurved; their bases are moderately thick and usually form a shallow cleft.

It may be possible with refined measurements of flower characters to separate some minor races of this species, but in the material examined variation between individuals scarcely exceeds variation within some single inflorescences.

Amaranthus viscidulus Greene.—

This species was described by Greene (1898, p. 344) from a specimen collected in the Sierra Blanca south of Carrizozo, New Mexico. It has since been collected only in the same mountains and a little to the north, near Pecos. Standley considered *A. viscidulus* as a synonym of *A. bracteosus* (1914, p. 508), but comparison of the type specimens shows little similarity in flower characters. Among other differences, *A. viscidulus* is uniformly 5-merous, while *A. bracteosus* has a reduced stamen number. *A. bracteosus* is here considered a synonym of *A. Powellii* (see below).

This species has a small unbranched terminal inflorescence, with a very prickly aspect because of the large bracts. The bracts and tepals are much like those of *A. retroflexus*, but the tepals are more strongly recurved and more extremely emarginate. The utricle cap has a distinctive large tower below the style-branches, which are unusually long.

Amaranthus Bigelovii Uline & Bray.—

This is another minor endemic species, described from western Texas by Uline and Bray (1894, p. 271). I have seen only the type specimen. As in *A. viscidulus*, there is only a small unbranched terminal inflorescence. The bracts are moderately large, with a narrow midrib. The tepals extend well beyond the small fruit; they are strongly recurved, definitely spatulate and emarginate, and somewhat indurated at the bases. The style-branches are erect and of medium length; their bases are slender and form a shallow cleft.

Amaranthus Brandegei Standley.—

This is another minor endemic species, described by Standley (1917, p. 109) from a plant collected in Sinaloa, Mexico. I have seen only the type and another specimen from Colima.

The individual cymes of the inflorescence are predominantly monochasial rather than dichasial; as a result the entire inflorescence has a lax, spindly aspect. The bracts are short, with a heavy midrib which does not extend far beyond the lamina. The tepals are about as long as the fruit, acute-tipped, definitely recurved, and heavily thickened at the base. The style-branches are very short and have especially thick bases.

The stamen number is uniformly 5, not 2–3 as stated in the original description.

Amaranthus scariosus Benth.—

The original description of this species (Bentham, 1844, p. 158) was accompanied by good drawings of the flowers, which leave no doubt as to the species characters. The type specimen was collected on Isla Tigre in the Gulf of Fonseca off the Honduras coast. Specimens have since been collected in the states of Guerrero, Vera Cruz, and Yucatan in Mexico, in Guatemala, El Salvador, Honduras, Nicaragua, and Costa Rica. The few specimens with habitat data were weeds of disturbed sites.

The terminal and lateral spikes of the inflorescence are moderately thick, very long, and erect. The entire inflorescence is large and showy, so that the plants look much more like cultigens than any of the other weed species. Except for its totally different inflorescence, the species is similar to *A. Bigelovii*. The bracts are fairly long, with a slender midrib extending into a moderately long point. The strongly recurved tepals extend well beyond the small fruit; in the mature flowers they become heavily indurated at their bases. The outer tepals are obovate and acutish at the tips, the inner definitely spatulate and emarginate. The utricle cap is extremely rugose above the line of dehiscence. The style-branches are of médium length and slightly recurved; their bases are slender and meet in a shallow cleft.

Amaranthus dubius Mart. ex Thellung.—

For a long time this species was erroneously given the Linnaean name *A. tristis* (Willdenow, 1798, p. 21; Moquin-Tandon, 1849, p. 260; etc.). Thellung's investigation of Linnaeus' specimens showed that the name *A. tristis* was originally applied to an entirely different entity (Thellung, 1912, p. 203; 1914, p. 265), and that there was no valid name available for this species. Thellung gave a full description of the species under the name *A. dubius*, previously published only as a *nomen nudum* by Martius (1814, p. 197). The name *A. dubius* has since been generally adopted for this species in herbarium determinations and published floras.

Amaranthus dubius is the common weed amaranth of the Caribbean; specimens are available from Cuba, Grand Cayman, Jamaica, Haiti, the Dominican Republic, Porto Rico, St. Croix, St. Thomas, Grenada, Trinidad, and Curaçao. On the mainland it has been found in the states of Campeche and Yucatan in Mexico; in Guatemala; Costa Rica; Panama; the departments of Antióquia, Santa Marta, Valle del Cauca, and Bolivar, in Colombia; Nueva Esparta in Venezuela; British Guiana; and in Surinam. Only a few collections are available from outside this area: one from a boat landing in Massachusetts, one from the port of Mazatlán on the west coast of Mexico, and a few from Hawaii and the Marshall Islands.

The spikes are quite variable in number and length; they are relatively slender and quite lax and soft-looking. The bracts are small, seldom exceeding the flowers; their midribs are slender and extend beyond the laminas in points. The tepals are about the same length as the mature fruits, incurved rather than recurved, and not indurated at the base. The outer tepals are oblong and acute-tipped, the inner obovate and obtuse-tipped. The small utricles have a relatively large tower below the style-branches, which are usually erect and long.

Amaranthus quitensis H.B.K.—

This species was described by Kunth (1817, p. 194) from plants collected in Ecuador. The original description is ambiguous and I have been unable to borrow the type material. The interpretation of the species here is based on the detailed description by Thellung (1914, p. 252), who had access to the Humboldt and Bonpland collection. About half of the specimens here included were labelled *A. quitensis* on the herbarium sheets; the others were given a wide variety of names.

This species is one of the most widespread weed amaranths of South America. It has been collected in the provinces of Buenos Aires, Córdoba, Formosa, Santiago del Estero, Tucumán, Salta, Jujuy, and Misiones in Argentina; in La Paz in Bolivia; in Ecuador; and in the Galapagos Islands.

The mature inflorescences are comparatively large, with many long lax lateral spikes. The bracts are long, with a moderately heavy midrib and moderately long point. The tepals are longer than the mature fruits and definitely recurved. The outer tepals are oblong or slightly obovate, and acute-tipped; the inner are obovate or broadly spatulate, and obtuse-tipped. The style-branches are usually erect and fairly long; their bases are rather slender and meet in a shallow cleft.

Amaranthus celosioides H.B.K.—

This is another species rather ambiguously described by Kunth (1817, p. 194), for which the type material is not available. The type collection was made in Venezuela. I have seen no Venezuelan material which agrees with the description of this species, but four specimens are available from Peru and Ecuador which can be tentatively assigned here. All of these were determined as *A. celosioides* by Standley and two were cited by him in a published flora of Peru (1937, p. 484).

All these specimens have the peculiar small bracts with very short points, used by Thellung (1914, p. 251) as the key character of the species. They also share a peculiar utricle cap, contracted into a narrow tower below the erect style-branches. In other characters the available specimens are extremely variable and some may be of hybrid origin. Additional collections and re-examination of the type are badly needed for better definition of this species.

Amaranthus hybridus L.—

Up to this point, few obvious intermediates between species have been encountered and definition of the species has been reasonably simple. Any hybridization which may occur between the species considered so far must be too infrequent to obscure the entities.

Nevertheless, the amaranths are notorious for their ability to hybridize. Accidental interspecific hybrids in great variety have been reported by many writers, from Willdenow (1798) and Regel (1849) to Thellung (1914, 1928) and Priszter (1949); various artificial crosses have been made by Murray (1938, 1940a, 1940b). Most of the accidental hybrids have been found in Europe, where species native to many different parts of the world have come into contact as weeds or been brought together in botanical gardens. In the regions under consideration here, few species have overlapping ranges, and the possible hybrid combinations are very limited. However, there is one species of section AMARANTHOTYPUS, *A. hybridus*, which has an especially wide range, overlapping that of various other species. Here, for the first time, we encounter variants which approach other species and cause serious difficulty in definition of the entity.

In the original description of *A. hybridus*, Linnaeus gave its home as Virginia (1753, 2:990), citing also Ray's earlier report of the plants as wild in New England. Linnaeus' species *A. hypochondriacus*, also attributed to Virginia and New England (1753, 2:991), was distinguished from *A. hybridus* only by having reddish rather than green pigmentation; it is generally regarded as synonymous with *A. hybridus* (Thellung, 1914, p. 241; Standley, 1917, p. 111).

About half of the specimens here included had been labelled *A. hybridus;* the rest had been given a wide variety of names, among which *A. chlorostachys* Willd. was prominent. This is one of the many names which Thellung reduced to synonymy with *A. hybridus*.

Northern Race of A. hybridus.—This race is common as a weed in the eastern United States and has been found at scattered places in the Old World. Specimens have been examined from Massachusetts, Connecticut, New York, New Jersey, Pennsylvania, the District of Columbia, Virginia, West Virginia, South Carolina, Florida, Mississippi, Ohio, Indiana, Kentucky, Illinois, Missouri, Arkansas, Kansas, Oklahoma, and Texas; also from Bermuda, the Bahamas, Japan, China, Algeria, Morocco, and Australia.

The inflorescences ordinarily have a great many short, crowded, lateral spikes, as in *A. retroflexus,* but the spikes are much less stiff and much less thick. The bracts are quite long, and the rather slender midribs extend far beyond the laminas. The tepals are about as long as the fruit, slightly recurved and often lightly indurated at the bases. The outer tepals are oblong and acute-tipped, the inner slightly obovate and acutish-tipped. The utricle cap narrows to a tower below the style-branches; the style-branches are erect and their bases are slender, meeting in a shallow cleft.

Individual specimens often show definite divergence from the norm of the race, both in superficial appearance and in flower characters. I believe that much of this variation is produced by introgression from *A. retroflexus*. Mass collections from weed amaranth populations around St. Louis (*J. D. Sauer 1473,* 50 plants; *1483,* 30 plants; etc.) include a continuous series of intermediates between the two

species. In some of these Missouri weed populations hybridization between *A. hybridus* and the genus *Acnida* is also indicated (*J. D. Sauer 1482*, 25 plants; etc.). Hybrids between *Amaranthus* and *Acnida* have been produced artificially by Murray (1940a).

Tropical Race of A. hybridus.—This race is a common weed from Mexico through Central America into northern South America and is scattered widely elsewhere. Specimens have been examined from the states of Nuevo León, San Luis Potosí, Nayarit, Jalisco, Colima, Michoacán, México, Puebla, Vera Cruz, Tabasco and Oaxaca in Mexico; from Guatemala; El Salvador; Costa Rica; the departments of Tachira, Mérida, and the Distrito Federal in Venezuela; La Paz and Cochabamba in Bolivia; the states of São Paulo and Minas Geraes in Brazil; the Dominican Republic; and Algeria.

In its inflorescence and flower characters, this race is much like the northern race of the species. The most tangible difference is in the utricle cap and style-branches. In the tropical race, the utricle cap tapers more gradually and is not constricted into a definite tower; the bases of the style-branches are farther apart and form more of a saddle than a cleft.

There is more variation between individual specimens included in this race than in any other of the entities examined. Even within what may be regarded as the core of the group, there are many subtle variants. Ranged around this indistinct core is a bewildering variety of divergent individuals, scarcely any two of which are exactly alike, even within a single collection. These specimens, not clearly assignable to any species, are not cited in the Specimens Examined on pages 620–623.

A few of these divergent individuals appear to be intermediate between *A. hybridus* and the grain species: *A. leucocarpus* is approached by some Mexican specimens (e.g. *J. D. Sauer 1313*), *A. cruentus* by some Central American specimens (e.g. *Standley 59046*). Other individuals approach some of the non-cultivated species of the section: *A. retroflexus* in northeastern Mexico (e.g. *Gregg 283*), *A. scariosus* in southern Mexico and Guatemala (e.g. *Pringle 6735*), *A. dubius* in Central America (e.g. *Pittier & Durand 3534*), and *A. quitensis* in Bolivia (e.g. *Bro. Julio 136*). Moreover, there is a bewildering series of forms, often labelled *A. hybridus* in herbaria, which appear to be intermediate between *A. hybridus* and species in other sections of the genus. This heterogeneous group includes specimens from wide areas of North, Central, and South America. Some of them diverge from typical *A. hybridus* in habit and inflorescence aspect, some have indehiscent fruits, almost all have reduced tepal or stamen number or both.

This complex of divergent forms related to *A. hybridus* cannot be satisfactorily analyzed here. Description and illustration of the collected variants, which probably represent only a small sample of the actual diversity, would require more space than all the preceding entities. Moreover, a much greater density of collections, together with mass samples of critical populations, are needed for an

understanding of this group. With the available material, I could do no more than speculate as to which variants are of hybrid origin and which are stable entities deserving taxonomic recognition.

Amaranthus Powellii S. Wats.—

This species characteristically has fewer than 5 stamens and therefore would be excluded from the section AMARANTHOTYPUS as usually defined. However, in other characters it is too close to some of the species of the section to be ignored here.

Like *A. leucocarpus*, *A. Powellii* was described by Watson (1875, p. 347) from plants grown at Harvard from Powell's wonderful packet of Arizona seeds. Unlike *A. leucocarpus*, this species has since been collected in abundance. It has been generally recognized by American workers (Uline and Bray, 1894, p. 313; Standley, 1917, p. 112; and others). A minor species from New Mexico, *A. bracteosus*, has been described as distinct from *A. Powellii* (Uline and Bray, 1894, p. 314), but examination of the type collections of both species reveals no impressive differences. I believe *A. bracteosus* should be reduced to a synonym of *A. Powellii*.

The specimens included here had mostly been labelled as either *A. Powellii*, *A. hybridus*, or *A. retroflexus* in about equal proportions.

Great Basin Race of A. Powellii.—This race, which includes the type of the species, is common as a weed and is occasionally reported in natural habitats over much of the western United States and northern Mexico. It has been found mostly at high elevations, often between 2,000 and 3,000 meters, in dry regions. Specimens are available from Wisconsin, Texas, Wyoming, Colorado, New Mexico, Arizona, Idaho, Utah, Washington, Oregon, California, and from the Mexican states of Coahuila, Chihuahua, and Baja California.

The inflorescences characteristically have a quite long, erect, terminal spike and a few erect lateral spikes; the spikes are thick and stiff and have a very prickly appearance from the exceptionally long bracts. The bracts are similar to those of *A. retroflexus*, with a very heavy midrib and a large lamina extending well toward the tip.

In other characters, this group is quite distinct from *A. retroflexus*. There are usually three or four stamens, although some flowers with five stamens can be found on a good many individuals. Tepal number in both staminate and pistillate flowers usually varies from four to five. The tepals are usually a little longer than the utricle, straight or slightly recurved, and somewhat indurated at their bases. The outer tepals are oblong or ovate, and acute-tipped; the inner are oblong or slightly obovate, and acutish or somewhat obtuse at the tips. The utricle cap tapers to the style-branches. The style-branches are of medium length and slightly recurved; their thick bases form a shallow cleft.

Variation in flower characters within this race is not great.

Cordilleran Race of A. Powellii.—This race is common as a weed in California and has been collected infrequently but very widely in Latin America, particularly at high elevations. Specimens are available from the states of Sonora, Chihuahua, San Luis Potosí, Tamaulipas, Michoacán, and Puebla in Mexico; Ecuador; Peru; Chile; La Paz in Bolivia; and Tucumán in Argentina.

This race is very similar to the preceding race in most characters, and probably cannot be clearly separated from it. It differs in having somewhat longer and more acute tepals, which are seldom recurved, and longer style-branches with thicker bases.

Other Closely Related Species.—

The existence of reduced stamen and tepal numbers in *A. Powellii,* as well as in some aberrant forms of *A. hybridus,* raises a question about the definition of the section AMARANTHOTYPUS.

The section was originally defined to include only a few adventive American species present in Europe; these were all sharply distinct from the native species. The section retains clear definition, as in Thellung's treatment (1914), only so long as consideration is limited to species present in the Old World. I know of no generally recognized or recognizable species peculiar to the Old World which is not distinguishable from all the species of AMARANTHOTYPUS by several qualitative characters. However, sharp definition of the section disappears when all the American species are considered. Among the New World endemics, there are a great many generally recognized species which are transitional; they are obviously closely related to AMARANTHOTYPUS, but lack one of the characters of the section. For example, *A. Palmeri* S. Wats., a common weed amaranth of the drier parts of the United States and Mexico, differs from species of AMARANTHOTYPUS chiefly by being dioecious; *A. Wrightii* S. Wats., a minor endemic of the southwestern states, differs only by its reduced stamen and tepal number; *A. chihuahuensis* S. Wats., a north Mexican endemic, only by its lack of a terminal spike; *A. ataco* Thellung, of Chile and Argentina, only by its indehiscent fruit. There are various similar examples of North and South American species which would be excluded from the section by a single character.

A considerable amount of material of these border-line species has been examined. None of it appears to be particularly close to any of the grain amaranths and it will not be discussed here. Once the rather arbitrary limits of the section AMARANTHOTYPUS are passed, there seems to be no natural stopping place short of a complete study of all the American species of *Amaranthus.*

III. CONCLUSIONS

The grain amaranths belong to several distinct but closely-related species, cultivated by a curiously diverse and scattered group of peoples since immemorially ancient times. Only a rough outline of the complex history of these ancient plants can be given in this preliminary survey.

In the Americas there are four major grain amaranth regions, each with its own peculiar cultivated species. *Amaranthus leucocarpus* dominates the great Mexican center and its tenuous extension into the southwestern United States. *Amaranthus cruentus* is cultivated in Guatemala, *A. caudatus* in the Andes, and *A. edulis* in Argentina. There seems to have been some diffusion of species betweén the Mexican and Guatemalan centers and between the Andean and Argentine centers, but on the whole the ranges of the species in the New World are distinct.

In Asia there is a great, vaguely delimited grain amaranth region stretching all the way from Manchuria through interior China and the Himalaya to Afghanistan and Persia. *Amaranthus leucocarpus* and *A. caudatus* are both grown throughout this area. The poorly known grain crop of Africa is probably also *A. caudatus*.

In mode of cultivation and use, the Old and New World crops are strikingly similar. In both areas the crop shows a special affinity for the highlands; so far as I know, its concentration at high elevations is not explainable by any natural barriers. Many wild amaranth species are common in the lowlands, and the grain species themselves are widely grown down to sea level as ornamentals. In both the Old and New World, the plants are usually grown on a small scale, mixed in the plantings of maize and other crops. The grain is ordinarily consumed by the growers and is prepared in similar ways almost everywhere. The seeds are first parched or popped; then they are either made into balls like popcorn, with a syrup binder, or they are ground to meal, which is stirred into a drink or baked into little cakes.

Taxonomically, all of the grain amaranths cultivated in the Old World are indistinguishable from certain of those cultivated in the New World. Not only in terms of species, but also in terms of sub-specific entities, the available Old World specimens represent nothing but a small sample of the diversity present in the American grain amaranths. There is an important group of cultivated amaranths which are obviously natives of Asia, including *A. tricolor, A. melancholicus, A. mangostanus, A. gangeticus*, etc. However, these are grown exclusively as pot-herbs or ornamentals, apparently never for the seeds. This entire Asiatic pot-herb group is easily distinguishable from the grain group by important technical characters, such as number of stamens, number of tepals, and shape of the tepals. Few of these Asiatic species are even superficially similar to the grain amaranths; for one thing, none of them has a branched terminal inflorescence.

The non-cultivated amaranths closely related to the grain species also show a striking concentration in the New World. There are many entities in this section of the genus which are endemic to the Americas; some are weeds, some appear to be truly wild. No evidence was found, either in the literature or in the herbarium, of any non-cultivated entity closely related to the grain amaranths which is peculiar to the Old World. Except in the Americas, members of this section of the genus are ordinarily found outside of cultivation only as sporadic adventive weeds.

The conclusion appears inescapable that the grain amaranths are all of New World origin. From which wild species they were derived is less clear. The grain species are all cultigens, unknown in the wild except as infrequent escapes. *Amaranthus leucocarpus* is morphologically fairly close to two non-cultivated species, *A. hybridus* and *A. Powellii,* both widespread in North and Central America. *Amaranthus cruentus* is more like *A. dubius* of Central America and the West Indies, while *A. caudatus* and *A. edulis* are closer to a South American wild species, *A. quitensis.* I am unable even to guess as to whether the cultigens were derived from these or similar wild species by simple selection or whether they are of complex hybrid origin.

The sharp taxonomic separation found between the cultivated species and their closest wild relatives was completely unexpected, since the frequency of hybridization in this genus is well known. The discontinuity may be explainable by the almost universal practice of selecting pale seeds for planting. No analysis of the genetics of the seed color is available, but it seems likely that the pale-seeded cultivated forms are simple recessives. If so, elimination of dark seeds in planting should be an effective barrier against introgression from wild species, which are without exception dark-seeded.

The cultigens differ from the wild species, not only in characters which are probably simple genetically, such as seed color, but also in quantitative characters, particularly those affecting grain yield. The higher yield of the cultivated species results mostly from the greater number of flowers and seeds produced, rather than from larger seed size. The cultigens are strikingly bigger in plant size than the wild species; they have more inflorescences per plant and the inflorescences are enormously larger and more compound. A well-developed grain amaranth produces such an enormous quantity of seed, though the seeds are individually minute, that the yield of the crop per unit area often exceeds that of maize, according to the few published statistics on yield and the opinions of Latin American farmers with whom I have talked.

Development of these stable entities so distinct from their wild relatives would be expected to require long selection. The antiquity of the crop is also indicated by other evidence. In both Asia and the Americas the crop has almost invariably been reported as a declining and disappearing relic, conserved mostly in remote primitive communities. Abundant direct evidence of the antiquity of the crop is available for the New World. In addition to the archaeologic cache of *A. caudatus* fruits found in South America, there are the magnificent early documentary records from Mexico. These indicate that grain amaranths were one of the great food staples of Mexico at the time of the Conquest, regarded by the people as among their most ancient crops, and fantastically important in legend and ritual.

The question as to whether the crop reached Asia before the European expansion cannot be answered with certainty. There is the 10th-century Chinese document which seems to refer to grain amaranths, but this is hardly absolute proof. If the crop was introduced into Asia after Columbus, it must be credited with a

remarkable achievement in making itself very much at home among strangers within a few generations. Of course, if these people were accustomed to cultivate one species of grain amaranth, rapid adoption of a second species would not be so remarkable. Of the two species grown for grain in Asia, *A. leucocarpus* is the more common and widespread and might be supposed to be more ancient in the area. Strangely enough, plants resembling *A. leucocarpus* do not appear in the European herbals until about 1700, more than a century after *A. caudatus* had been brought to Europe as an ornamental.

We have seen that the practice of cultivating grain amaranths is old and deep in various cultures. I believe these plants deserve special consideration by those willing to speculate about the very beginnings of agriculture. Various workers have inclined to the idea that the transition of plants from wild to domesticated was not always accomplished in a single step by deliberate domestication. In many cases wild plants may have become weedy camp-followers and entered cultivation gradually through a long process of modification by largely unconscious human selection. One version of this concept has been well expressed by Frazer (1912, 1:128). He postulated that by digging up the soil in a search for roots, ancient man produced favorable growing plots for his wild food seeds, dropped accidentally during winnowing or other operations. A slightly different version than Frazer's would involve the accidental establishment of useful plants on village refuse heaps. In either case, by continued harvesting and accidental sowing, plants able to persist in such disturbed habitats might become domesticated by imperceptible degrees. The amaranths are attractive candidates for such accidental domestication; the seeds of the wild species are often gathered and eaten by primitive peoples and the plants are notoriously successful weeds of disturbed habitats.

Following another line of reasoning, Carl Sauer (1936, p. 292) pointed out that the presence side by side in an area of two starch crops, one localized and the other of wide range, suggests that the local crop is older in the area; it can survive as a relic because of tradition and the inertia of habit. "Qualities that are insufficient to cause the development side by side of two similar foodstuffs from different wild ancestors may be sufficient to keep one in use if a more valuable crop is brought in from another area." This line of reasoning suggests that grain amaranths, at least in some areas, are relics of an ancient staple starch crop, largely supplanted by a later arrival, maize.

Such speculations will obviously need additional support from factual evidence if they are to become more than hypotheses. Such evidence may eventually come from analysis of pollen deposits. Deevey (1944, p. 149) made a suggestive preliminary pollen analysis of sediments in Lake Pátzcuaro in Michoacán, Mexico. He estimated that the sediments are now accumulating at the rate of about one meter in 400 years, but that deposition was probably slower in the past. Maize and agave pollen were found down to depths of between four and five meters. About a meter lower, he found that there had been a sudden increase in deposition of a type of pollen identified only as coming from either chenopods or amaranths. More

precise identification of this pollen would be extremely interesting. It may be derived from wild amaranths or chenopods, as Deevey assumes. On the other hand, it may mark the coming of an agriculture based on grain amaranth cultivation. When the first Spanish conquerors arrived on the shores of this same lake, some thousands of years after this pollen was deposited, they found that the Indians had the custom of making little figures of amaranth meal for the festival of their earth goddess, giver of all crops.

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PERSONS CITED

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LIST OF SPECIMENS EXAMINED

Supposed hybrids and specimens of *Amaranthus* without collector's numbers are not cited. Letters in parentheses refer to herbaria from which the specimens were obtained: GH—Gray; MO—Missouri Botanical Garden; UC—University of California; US—U. S. National; X—undistributed specimens. Italicized letters refer to species determinations: *Bi—A. Bigelovii; Br—A. Brandegei; Ca—A. caudatus; Ce—A. celosioides; Cr—A. cruentus; D—A. dubius; E—A. edulis; H—A. hybridus; L—A. leucocarpus; P—A. Powellii; Q—A. quitensis; R—A. retroflexus; S—A. scariosus; V—A. viscidulus.*

United States and Canada.—

Abrams, L. R. *2963* (MO) *P.*
Allard, H. A. *9606* (MO) *H.*
Allen, Paul. *142* (MO) *P.*
Anect, Bro. *138* (MO) *P.*
Arthur, J. C. *8* (MO) *R.*
Austin, S. W. *372* (UC) *R.*
Baker, C. F. *303* (MO) *P.*
Baker, Earle & Tracy. *486* (MO) *P.*
Ball, C. R. *531* (MO) *R; 588* (MO) *R.*
Bechtel, A. R. *8057* (MO) *R.*
Bell, W. B. *280* (MO) *R.*
Benke, H. C. *5798* (MO) *H; 5799* (MO) *R.*
Berkley, E. E. *1283* (MO) *R; 1482* (MO) *H.*
Blumer, J. C. *1404* (MO) *P.*
Boettcher, F. L. J. *209* (MO, UC) *R.*
Booth, L. M. *1295* (UC) *P.*
Bowerman, M. L. *3539* (UC) *R; 3727* (UC) *R.*
Braunton, E. *705* (UC) *P; 720* (UC) *P; 1105* (MO) *R.*
Brooks, S. C. *1065* (UC) *H.*
Burk, M. *670* (MO) *R.*
Bush, B. F. *316* (UC) *H; 317* (UC) *R; 428* (MO) *H; 447* (MO) *H; 476* (MO) *H; 485* (MO) *R; 789* (MO) *H; 8104* (MO) *R; 8108* (UC) *R; 9050C* (UC) *R; 13118* (MO) *H; 13119* (MO) *H; 13173* (MO) *H; 13174* (MO) *H; 13208* (MO) *H; 13209* (MO) *H; 15772* (MO) *H; 15782* (MO) *H.*
Carr, W. P. *142* (MO) *R.*
Clark, J. A. *141* (MO, UC) *R, P.*
Clarke, D. G. *58* (MO) *R.*
Clemens, J. *11561* (MO) *R.*
Coghill, G. E. *161* (MO) *P.*
Cooke, W. B., II. *553* (UC) *P.*
Coues & Palmer. *41* (MO) *P.*
Cowen, J. H. *2153* (UC) *R.*
Craig, M. *4411* (UC) *R.*
Cronquist, A. *3429* (MO) *P; 3831* (MO) *P.*
Curtiss, A. H. *4982* (MO) *H.*
Cutak, L. & Christ, A. *100* (MO) *R.*
Darrow, Phillips & Pultz. *1179* (UC) *P.*
Davis, J. *591* (MO) *H; 2025* (MO) *H; 2078* (MO) *R; 3031* (MO) *H; 3473* (MO) *H; 4028* (MO) *H.*
Davy, J. B. *4044* (UC) *P; 7050* (UC) *P.*
Demaree, D. *7563* (MO) *R; 8427* (MO) *H; 8801* (MO) *H; 13261* (MO) *R; 13405* (MO) *R; 18459* (MO) *H; 20398* (MO) *H; 21675* (MO) *H.*
Dudgeon, W. S. *17* (MO) *R.*
Ellis, C. C. *146* (MO) *P.*
Fendler, A. *735* (MO, US) *P; 736* (MO) *R.*
Fogg, J. M., Jr. *1402* (MO) *R.*
Gates, F. C. *18859* (MO) *R.*
Goehring, G. H. M. *67* (MO) *H.*
Goodner & Henning. *1157* (MO) *P.*
Gould & Hudson. *3788* (UC) *P.*
Gould & Robinson. *4998* (UC) *P.*
Grant, G. B. *1718* (MO) *P; 6577* (MO) *P.*
Greenman, J. M. *1599* (MO) *H.*
Greenman & Greenman. *3733* (MO) *H.*
Hansen, G. *1260* (MO) *P; 1411* (UC) *P.*
Hanson, H. C. *A157* (MO) *P.*
Harrison & Harrison. *8573* (MO) *P.*
Heiser, C. B., Jr. *1919* (UC) *R.*
Heller, A. A. *1765* (MO, UC) *R; 12199* (MO) *R.*
Heller & Heller. *3428* (MO, UC) *P.*
Hoover, R. F. *99* (UC) *R.*
House, H. D. *29425* (MO) *H; 30165* (MO) *R.*
Johnston, E. L. *287* (MO) *R.*
Jones, M. E. *3977* (MO, UC, US) *P; 6050g* (MO, UC) *P.*
Kellogg, J. H. *511* (MO) *H; 888* (MO) *H.*
Kerr, M. *46* (UC) *P.*
Killip, E. P. *40186* (MO) *H.*
Leiberg, J. B. *1550* (MO, UC) *P.*
Mackensen, B. *10* (MO) *R.*
Mackenzie, K. K. *4775* (MO) *H.*
McKnight, K. *10704* (UC) *P.*
Mead, S. B. *14* (MO) *H.*
Metcalf, F. P. *1342* (MO) *R; 6395* (MO) *H.*
Meyer, F. G. *786* (MO) *P.*

Moldenke, H. N. *499* (MO) *H.*
Moore, A. H. *355* (UC) *R*; *4351* (GH) *L.*
Mueller, C. H. *7986* (MO) *P.*
Muenscher, W. C. *16104* (UC) *P.*
Mulford, A. I. *381* (MO) *P*; *747* (MO) *R.*
Nelson, A. *8079* (MO) *P.*
Norton, J. B. *424* (MO) *R*; *425* (MO) *H.*
Orcutt, C. R. *5868* (MO) *R.*
Palmer, E. 1875:319 (UC) *P*; *1892:2716* (UC) *R.*
Palmer, E. J. *427* (MO) *H*; *2624* (MO) *H*; *3114* (MO) *R*; *12292* (MO) *R*; *30741* (MO) *P*; *46377* (MO) *R.*
Pammel, L. H. *48* (MO) *R*; *3863* (MO) *R.*
Parish, S. B. *11657* (UC) *P.*
Parry, Bigelow, Wright & Schott. *1190* (US) *Bi.*
Pendleton, R. L. *191* (UC) *P.*
Redfield, J. H. *7020* (MO) *H.*
Reverchon, J. *1756* (MO) *R*; *2939* (MO) *R.*
Ricksecker, A. E. *60* (UC) *R.*
Rydberg & Imler. *647* (MO) *R.*
Sauer, J. D. *1189* (X) *H*; *1237* (MO) *P*; *1238* (MO) *R*; *1459* (X) *H*; *1469* (MO, UC) *R*; *1470* (MO, UC) *P*; *1471* (UC) *R*; *1472* (MO, UC) *P.*
Schreiber, B. O. *741* (UC) *P.*
Sherff, E. E. *1845* (MO) *R.*
Standley, J. P. *232* (MO) *R.*
Standley, P. C. *4535* (MO) *P*; *4891* (MO) *P*; *4918* (MO) *P*; *5149* (MO, US) *V.*
Stanford, E. E. *703* (GH) *Cr.*
Stevens, G. W. *859* (MO) *R*; *1841.2* (MO) *H.*
Steyermark, J. A. *8875* (MO) *H*; *8972* (MO) *R.*
Thompson, C. H. *137* (MO) *R.*
Thompson, J. W. *3664A* (MO) *P.*
Tracy, S. M. *2170* (MO) *H*; *2173* (MO) *H.*
Wahl, H. A. *4763* (UC) *P*; *6257* (UC) *P.*
Walker, H. A. *772* (UC) *P.*
Waugh, —. *164* (MO) *R.*
Wiegand, K. M. *6396* (GH, MO) *L.*
Wislizenus, F. *357* (MO) *H.*
Wooton, E. O. *73* (MO,UC) *R*; *300* (US) *V*; *3950* (US) *V.*
Wright, C. *1748* (MO) *P*, in part.

Mexico and Central America.—

Allen, P. H. *874* (US) *D.*
Alvarez, C. *749* (GH) *H.*
Arsène, Bro. G. *374* (US) *Cr*; *397* (US) *P*; *1052* (US) *P*; *2300* (MO, US) *P.*
Baker, —. *2873* (UC, US) *Cr.*
Botteri, M. *261* (US) *H*; *332* (GH) *H*; *401* (GH) *H*; *553* (GH, US) *H*; *555* (GH) *H.*
Calderón, S. *739* (US) *Cr*; *2090* (US) *S.*
Cooper, J. J. *68* (US) *H.*
Deam, C. C. *210* (GH) *S.*
Erlanson, C. O. *350* (US) *D.*
Ervdenberg, L. C. *283* (GH) *H.*
Fisher, G. L. *45129* (US) *P.*
Garnier, A. *369* (US) *S*; *371* (US) *Cr*; *525* (US) *S*; *1765* (GH) *S.*
Gaumer, G. F. *1788* (MO) *D*; *1789* (MO) *D*; *23548* (MO) *S*; *23550* (MO, UC, US) *D*; *23735* (UC) *S*; *23789* (US) *D*; *24065* (MO) *D.*
Gentry, H. S. *1843* (MO, UC) *L*; *1844* (US) *L*; *6547* (MO) *L.*
Gonzalez & Conzatti. *909* (GH) *Cr.*
Grant, V. *934* (GH) *S.*
Hernandez X., E. *3715* (X) *L.*
Heyde, E. T. *720* (US) *H.*
Hinton, G. B. *2137* (MO, US) *L*; *3015* (GH, US) *H*; *13584* (GH) *H.*
Hunter & Allen. *712* (MO) *D.*
Hunziker, A. T. *2948* (GH) *L.*
Johnson, H. *839* (US) *Cr.*
Johnston, I. M. *8342a* (GH) *R.*
Killip, E. P. *3209* (US) *D*; *3432* (US) *D.*
Le Sueur, H. *611* (GH, MO) *P*; *612* (GH) *P.*
Lumholtz, C. *1041* (GH, US) *P.*
Lundell, C. L. *5200* (US) *P.*
Martinez-Calderón, G. *96* (US) *H.*
Mell, C. D. *2070* (US) *D.*
Mexia, Y. *41* (MO) *D.*
Meyer & Rogers. *2814* (X) *P.*
Padilla, S. A. *148* (MO, US) *S*; *421* (US) *S.*
Palmer, E. *1880:1128* (US) *R*; *1880:-2043* (GH) *R*; *1886:626* (MO) *H*; *1886:629* (US) *H*; *1886:630* (MO) *H*; *1886:694* (US) *L*; *1886:695* (US) *L*; *1891:1000* (GH) *Br*; *1891:1718* (US) *Cr*; *1892:1883* (US) *H*; *1892:1884* (GH) *H*; *1894:142* (US) *S*; *1897:126* (US) *H.*
Parry & Palmer. *785½* (GH, MO) *H.*
Paul, Bro. *76* (US) *D.*

Piper, C. V. *5782* (US) *D.*
Pittier, H. *197* (US) *L; 3610* (US) *D; 6859* (US) *D.*
Pringle, C. G. *2179* (GH) *P.*
Purpus, C. A. *7787* (UC) *H; 8665* (MO, UC, US) *S; 8871* (MO, UC) *H; 10831* (US) *H.*
Renson, C. *288* (US) *H.*
Rovirosa, J. N. *744* (US) *H.*
Sauer, C. O. *28* (MO, UC) *H.*
Sauer, J. D. *1010* (MO) *Ca; 1112* (MO, UC) *P; 1133* (X) *H; 1141* (X) *H; 1150* (MO) *H; 1153* (MO) *H; 1155* (X) *H; 1161* (MO) *L; 1162* (MO) *L; 1168* (X) *Cr; 1170* (MO) *L; 1171* (MO) *L; 1172* (MO) *Cr; 1173* (MO) *L; 1174* (MO) *L; 1175* (MO) *Cr; 1176* (MO) *Cr; 1177* (X) *Cr; 1193* (MO) *L; 1239* (X) *L; 1240* (MO) *Cr; 1265* (MO) *Cr; 1266* (MO) *Cr; 1267* (X) *Cr; 1274* (X) *L; 1277* (X) *L; 1285* (MO) *Cr; 1311* (X) *Cr; 1355* (MO) *L.*
Schery, R. W. *131* (MO) *P.*
Seaton, H. E. *19* (GH) *H.*
Smith, C. L. *1768* (GH) *H.*
Solis Rojas, F. *250* (MO) *H.*
Standley, P. C. *19238* (US) *Cr; 20712* (MO, US) *S; 20833* (MO, US) *S; 21111* (US) *S; 24286* (US) *D; 25670* (US) *D; 26107* (US) *D; 26891* (US) *D; 27101* (US) *D; 28192* (US) *D; 28517* (US) *D; 29840* (US) *Cr; 30135* (US) *D; 30254* (US) *D; 30596* (US) *Cr; 31485* (US) *D; 37004* (US) *D; 39028* (US) *D.*
Standley & Valerio. *44258* (US) *S.*
Stanford, Retherford & Northcraft. *173* (MO) *P; 505* (UC) *P.*
Stork, H. E. *89* (US) *D.*
Tonduz, A. *7118* (US) *H; 13704* (US) *S.*
Townsend & Barber. *238* (MO, US) *P.*
Tuerckheim, H. von. *11774* (US) *Cr.*
Wedel, H. von. *2854* (MO, US) *D.*
White, G. *119* (MO) *D.*
White, S. S. *1592* (GH) *H; 3393* (GH) *P.*
Wiggins & Demaree. *4789* (UC, US) *P.*
Wiggins & Gillespie. *4114* (MO, US) *P.*
Wislizenus, F. *215* (MO) *Cr.*

West Indies.—

Barreto, M. *4* (US) *Cr.*
Broadway, W. E. *5553* (GH, MO, UC) *D; 6802* (GH, MO, US) *D; 7967* (MO) *D.*
Brown, S. *538* (US) *H.*
Brown & Britton. *370* (US) *H.*
Brown, Britton & Bisset. *1989* (US) *H; 2231* (US) *H.*
Collins, F. S. *111* (GH) *H; 188* (GH) *H; 189* (US) *H.*
Curran & Haman. *66* (UC) *D.*
Ekman, E. L. *H9828* (US) *Cr; H12616* (US) *Cr; H13914* (US) *H.*
Hermann, —. van. *5102* (US) *D.*
Holdridge, L. R. *1025* (US) *Cr.*
Jack, J. G. *6119* (US) *D.*
Leonard, E. C. *7619* (US) *Cr; 8359a* (UC, US) *D; 9410* (MO) *D.*
Leonard & Leonard. *15302* (US) *Cr.*
Moore, A. H. *2948* (GH) *H.*
Orcutt, C. R. *323* (UC) *D; 1869* (UC) *D; 2722* (UC) *D.*
Otero, J. I. *48* (MO) *D.*
Ricksecker, A. E. *109* (MO, UC, US) *D; 332* (MO) *D.*
Robinson, B. L. *37* (GH) *H.*
Shafer, J. A. *12045* (MO) *D.*
Sieber, F. W. *159* (MO) *D.*
Sintenis, Bro. *3553* (GH) *D.*
Stevenson, J. A. *5298* (US) *Cr.*
Valeur, E. J. *231* (MO) *D.*
Wilson, P. *392* (US) *D.*

South America.—

Archer, W. A. *2677a* (US) *D.*
Ariste-Joseph, Bro. *A359* (US) *Cr.*
Bang, A. M. *97* (GH, MO, US) *P; 231* (US) *H; 732* (US) *H*, in part.
Barkley, Barros & Alvarez. *395* (X) *D.*
Bartlett, H. H. *20319* (US) *Q.*
Buchtien, O. *3166* (US) *Q; 3168* (GH, US) *Q; 4198* (GH) *H; 5402* (US) *Ca; 8785* (US) *P.*
Campos Novaes, J. de. *430* (US) *Cr.*
Cardenas, M. *3512* (GH, US) *Ca; 3513* (GH) *Ca; 3514* (GH) *Ca; 3515* (GH) *Ca; 3516* (GH) *H.*
Cook & Gilbert. *256* (US) *Ca.*
Cuatrecasas, J. *14471* (MO) *D.*
Daniel, Bro. *447* (US) *D.*
Ekman, E. L. *117* (US) *Q; 118* (GH) *Q.*
Elias, Bro. *1483* (US) *Cr.*
Fendler, A. *1760* (GH) *H; 2386* (GH) *Cr, D.*
Firmin, Bro. G. *214* (US) *P.*
Grisales, A. *11* (X) *Cr.*
Hassler, E. *12506* (MO, US) *Q.*
Heriberto, Bro. *56* (US) *D.*
Herrera, F. L. *1053* (GH, US) *P; 1073* (US) *P.*
Herter, G. *54* (UC) *Q; 54a* (MO) *Q; 54b* (US) *Q; 805* (GH) *Q.*

Houk, W. G. *61* (US) *H.*
Huidoho, K. de. *439* (US) *Q.*
Hunziker, A. T. *810* (US) *Ca; 1085* (GH) *Ca; 2127* (GH) *E; 2128* (GH) *Ca; 3003* (MO) *E.*
Jörgensen, P. *2563* (US) *Q; 2574* (MO, US) *Q; 3441* (MO, US) *Q.*
Killip & Smith. *21926* (US) *Ce.*
Krapovickas, A. *2260* (GH) *Q.*
Lehmann, F. C. *7702* (GH, US) *Cr.*
Mandon, G. *1018* (GH) *Q*, in part.
Mille, A. *46* (GH) *Ce.*
Miller & Johnston. *30* (MO) *D.*
Monetti, —. *1311* (GH) *Q; 1653* (GH) *Q; 1718* (GH) *Q; 2271* (GH) *Q.*
Montero, G. *2303* (GH) *P.*
Morong, T. *980* (UC, US) *Q.*
Noguera, J. M. *49* (GH) *D.*
Pachano, A. *171* (GH, US) *Cr.*
Parodi, L. R. *8910* (GH) *Q.*
Peirano, —. *9666* (GH) *Q.*
Pennell, F. W. *4668* (GH) *D.*
Pickel, B *3268* (US) *Cr.*
Potter, D. *5334* (GH) *D.*
Rodriguez, —. *185* (GH) *Q.*
Santoro, J. *408* (US) *H; 485* (US) *H.*
Sauer, J. D. *1179* (X) *Ca; 1241* (MO) *Ca; 1283* (MO) *Ca; 1298* (X) *Ca; 1314* (X) *Ca; 1315* (X) *Ca.*
Smith, H. H. *1194* (UC) *D; 1195* (MO) *D.*
Snodgrass & Heller. *219* (GH) *Q.*
Soukup, J. *1999* (US) *P.*
Steinbach, —. *2793* (GH) *H.*
Tamayo, F. T. *513* (US) *H; 2472* (US) *H.*
Tomas, Bro. *906* (US) *D.*
Venturi, S. *1954* (US) *Q*, in part; *1955* (US) *Q; 2044* (US) *Q; 4234* (GH) *Q; 6038* (MO, US) *Q; 10316* (GH) *Q.*
Weberbauer, A. *5332* (GH) *Ce.*
Williams, L. O. *5653* (GH) *Cr.*
Williams & Assis. *6461* (GH) *H.*

Asia.—

Amdursky, J. *231* (US) *R.*
Beach, K. H. *47* (UC) *R; 125* (UC) *R.*
Boeea, R. S. *6491* (GH) *Cr; 8022* (GH, US) *Cr; 8710* (GH) *Cr.*
Castro & Melegrito. *144* (UC) *Cr.*
Chen, F. H. *369* (GH) *Ca.*
Chen, Y. *803* (UC) *L; 898* (UC) *L; 928* (UC) *L.*
Chiao, C. Y. *333* (UC) *L; 1183* (UC, US) *Cr; 3143* (UC) *L.*
Ching, R. C. *4668* (UC, US) *Cr.*
Clemens & Clemens. *3309* (UC, US) *Cr.*
Cowgill, W. H. *2087* (GH) *Ca; 2354* (GH) *L; 2355* (GH) *L.*
Devore & Hoover. *112* (US) *Cr.*
Dorsett & Dorsett. *4089* (UC, US) *L.*
Elliott, E. *14* (GH, US) *H.*
Fang, W. P. *3242* (GH, US) *L.*
Feng, H. T. *16* (UC) *Cr.*
Field & Lazar. *807* (GH, US) *R; 997* (GH, US) *R.*
Groff, G. W. *711* (UC) *Ca.*
Henry, A. *2732* (US) *L; 4808* (GH) *L.*
Hooker, J. D. *2435* (GH) *L.*
Koelz, W. *7279* (US) *L.*
Liu, J. C. *823* (UC) *R; 1716* (UC) *R.*
Maire, E. E. *503* (UC) *L; 504* (UC) *L; 509* (UC) *H; 712* (UC) *L.*
McClure, —. *3345* (UC) *Cr.*
Merrill, E. D. *8501* (US) *Cr.*
Ritchie, —. *631* (GH) *L.*
Rock, J. F. *6283* (UC, US) *L.*
Sauer, J. D. *1310* (X) *Ca; 1484* (MO) *L; 1489* (MO) *L; 1492* (X) *L; 1495* (MO) *L; 1499* (X) *L; 1503* (MO) *Ca; 1505* (MO) *Ca.*
Schlagintweit, —. *1486* (GH) *Ca; 1958* (GH) *L; 3293* (GH) *L; 9364* (GH) *L; 12075* (GH) *L; 2:1353* (UC) *L; 2:4365* (UC) *L; 4:871* (UC) *L; 4:872* (US) *Ca; 4:5787* (US) *Ca; 4:5789* (US) *L; 4:6407* (US) *L; 4:13177* (US) *L.*
Shiota, K. *2667* (GH) *Ca; 2670* (GH) *Cr; 2672* (GH) *R.*
Steward, Chiao & Cheo. *784* (GH, US) *L.*
Stewart, R. R. *19656* (GH) *L; 21360* (GH) *R.*
Strachey & Winterbottom. *2* (GH) *Ca,L.*
Vvedensky, —. *425* (MO) *R.*
Zimmerman, —. *254* (US) *L.*

Africa.—

Craine, —. de. *736* (GH) *Ca.*
Dümmer, R. *532* (US) *Cr; 590* (US) *Cr.*
Jamin, P. *207* (GH) *H.*
Lebrun, J. *789* (GH, US) Cr.
Lynes, H. *596* (US) *Ca.*
Mearns, E. A. *1011* (US) *Cr; 1377* (GH, US) *Cr; 2403* (US) *Cr.*
Quer, Font. *121* (UC) *H.*
Schimper, W. *276* (UC, US) *Ca; 359* (MO) *Ca; 1077* (MO, US) *Ca; 1513* (GH, MO) *Ca; 1535* (GH, MO, US) *Ca.*
Warion, A. *1360* (MO) *H.*

Oceania.—

Degener & Topping. *17896* (MO) *Cr.*
Fosberg, F. R. *13348* (MO) *D; 13830* (MO) *D; 24390* (X) *D; 26503* (X) *D; 26935* (X) *D.*
Seemann, B. *367* (GH) *Cr.*
White, C. T. *10762* (GH) *H.*

Explanation of Plate

PLATE 10

A, Xochihuauhtli (Sahagún, ca. 1570a, 5:137).

B, Tlapalhuauhtli (Sahagún, *ibid.* 137).

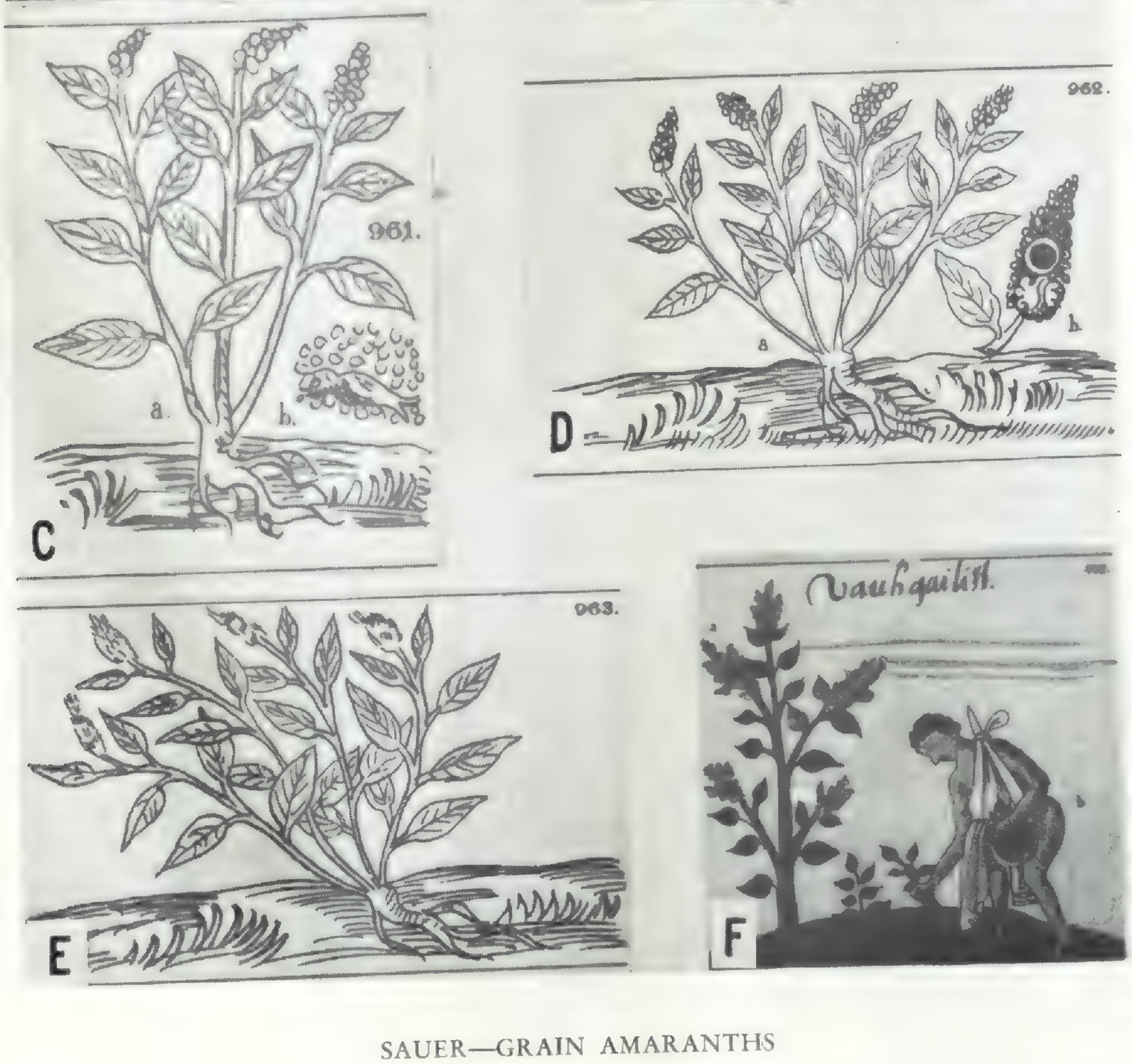
C, Michihuauhtli (Sahagún, *ibid.* 138).

D, Tezcahuauhtli (Sahagún, *ibid.* 138).

E, Petzícatl (Sahagún, *ibid.* 138).

F, Huauhquilitl (Sahagún, *ibid.* 102).

956.
a
b.
A
957.
B


961.
a.
b.
C
962.
a
b
D

963.
E
Vauhquilin.
F

SAUER—GRAIN AMARANTHS

EXPLANATION OF PLATE

PLATE 11

A, Young grain amaranths near San Gregorio Atlapulco, D. F.

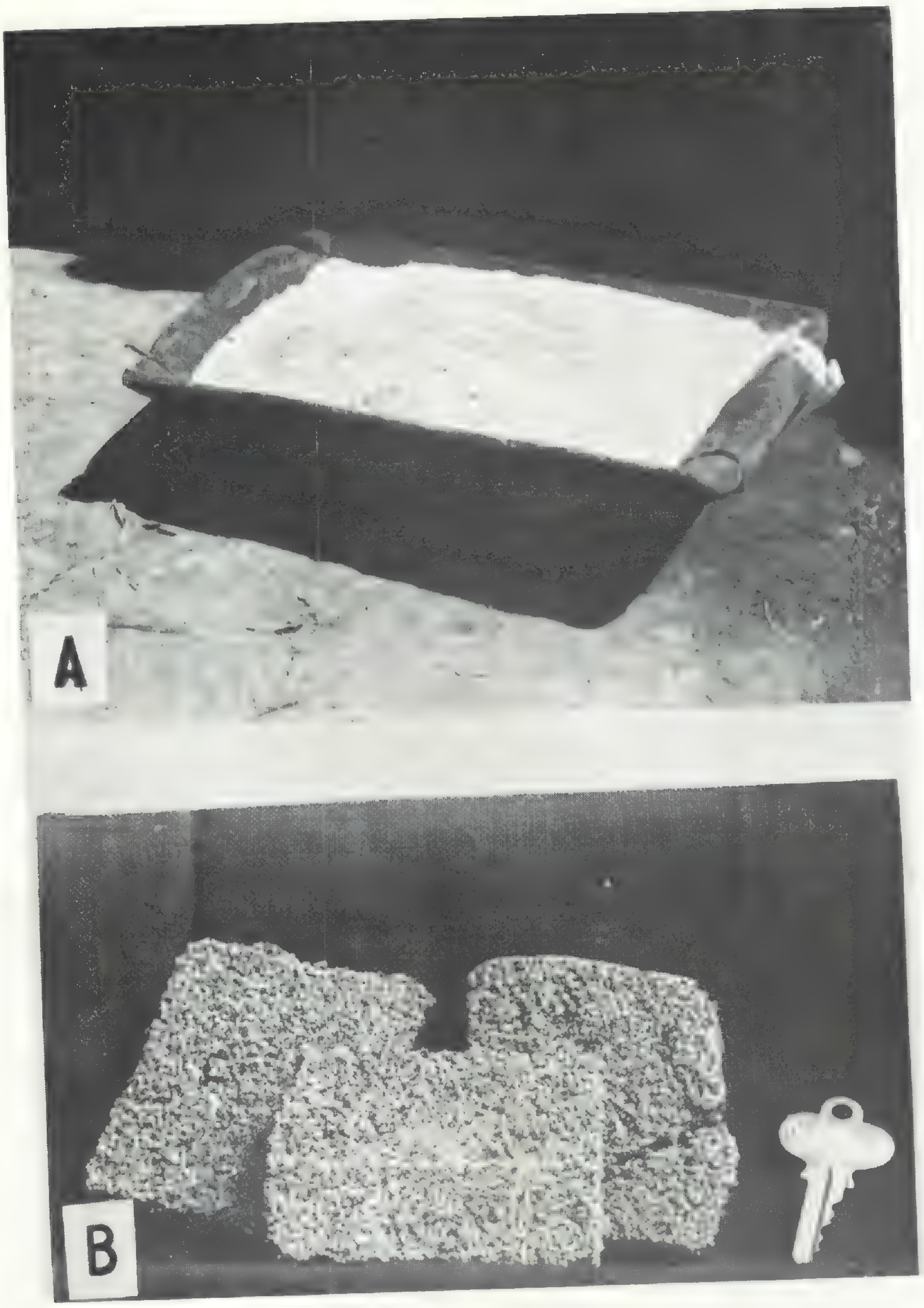
B, Transporting harvested amaranths, Tulyehualco, D. F.

EXPLANATION OF PLATE

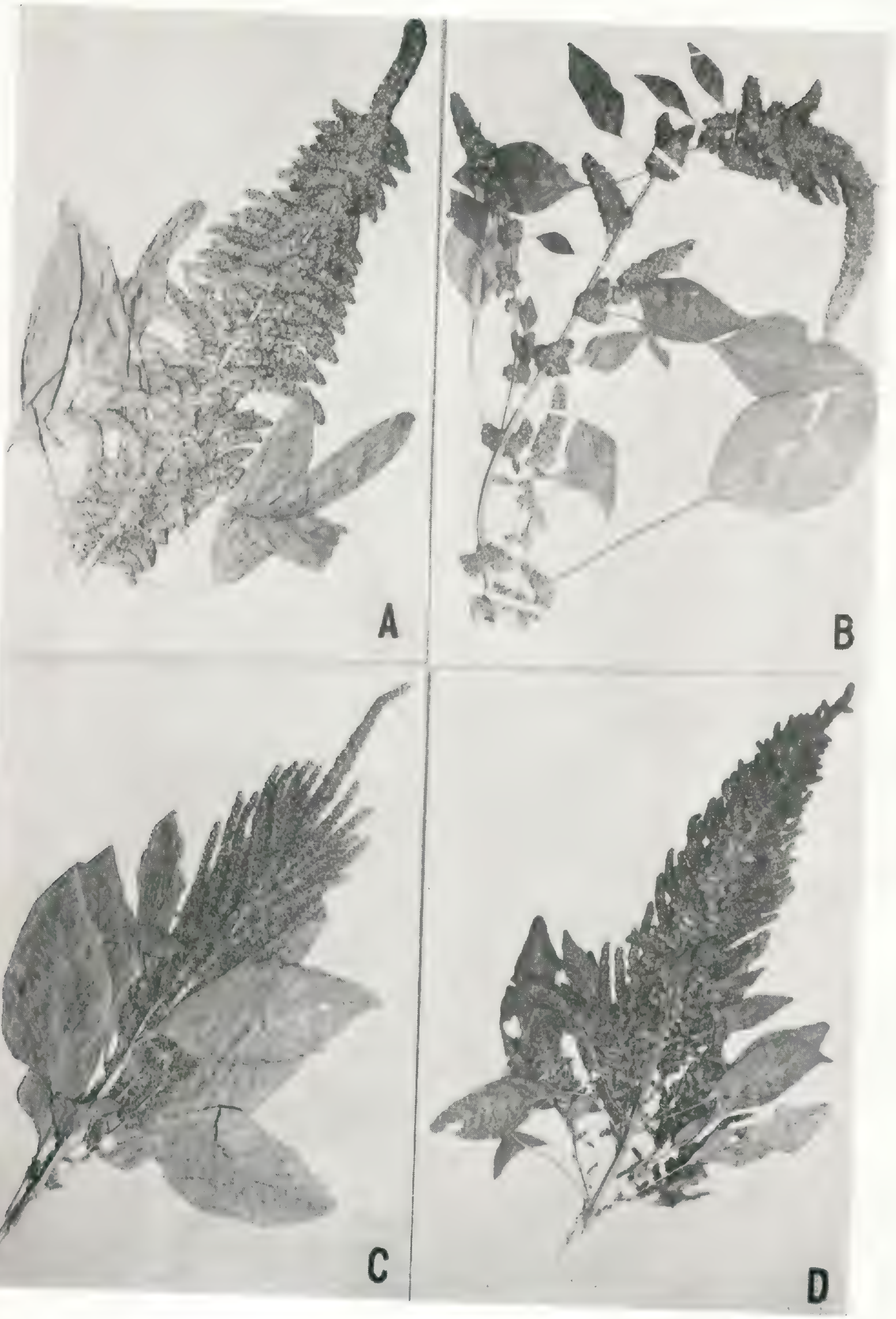
PLATE 12

A, Popped amaranth seed prepared for *niguas*, San Martín Jilotepeque, Chimaltenango.

B, *Niguas* made at San Juan Sacatepéquez, Guatemala.



SAUER—GRAIN AMARANTHS


A
B
C
D

Explanation of Plate

PLATE 14

A, Inflorescence of *A. cruentus*, Mexican race, × ¼. (Specimen: *J. D. Sauer 1266-A*).

B, Inflorescence of *A. caudatus*, ×¼. (Specimen: *M. Cárdenas 3513*).

C, Inflorescence of *A. edulis*, × ¼. (Specimen: *A. T. Hunziker 2127*).

Explanation of Plate

PLATE 13

A, Inflorescence of *A. leucocarpus*, common race, × ¼. (Specimen: *J. D. Sauer 1162-E*).

B, Inflorescence of *A. leucocarpus*, Arizona race, × ¼. (Specimen: *J. W. Powell s. n.*, type of the species).

C, Inflorescence of *A. leucocarpus*, aberrant race, × ¼. (Specimen: *J. D. Sauer 1355-B*).

D, Inflorescence of *A. cruentus*, common race, × ¼. (Specimen: *J. D. Sauer 1240-B*).

SAUER—GRAIN AMARANTHS

Appendix

EXTRACTS FROM EARLY LATIN AMERICAN SOURCES

(Figures in parentheses refer to pagination of editions cited in List of Sources.)

A. *ANONYMOUS, CA. 1540.*—

(20). Iba esta diosa [Cueravaperi] dos fiestas con sus sacerdotes á la ciudad de Mechuacan por la fiesta de Cuingo y Corindaro . . . Era tenida en mucho en toda esta provincia, y nombrada en todas sus fabulas y oraciones, y decían que era madre de todos los dioses de la tierra, y que ella los envió â morar á las tierras, dándoles mieses y semillas que trujesen.

(108). Luego como vieron los indios los españoles, de ver gente tan estraña y ver que no comían sus comidas de ellos, y que no se emborrachaban como ellos, llamábanlos tucupacha, que son dioses . . . y á los caballos llamaban venados, y otros tuycen, que eran unos como caballos que ellos hacían en una su fiesta de Cuingo, de pan de bledos.

B. *ANONYMOUS, CA. 1550.*—

Cap. I (128). Las mozas deste recogimiento, dos días antes de la fiesta deste ídolo, Huitzilopuchtli, molían mucha cantidad de semilla de bledos juntamente con maíz tostado, y después de molido, amasábanlo con miel, y hazían de aquella masa un ídolo tan grande como era el de madera . . . Hecho esto, salían todas las doncellas con el aderezo referido y sacaban de su recogimiento unos trozos de massa de maíz tostado, y bledos que es la mesma de que el ídolo era hecho, hechos á manera de huevos grandes, y entregábanlos á los mancebos, y ellos subíanlos arriba, y ponían los á los pies del ídolo por todo aquel lugar hasta que no cabían mas: á estos trozos de masa llamaban los huessos y carne de Huitzilopuchtli.

C. *SAHAGUN, CA. 1570b.*—

Libro 1, Cap 13 (1:30). A este dios [Xiuhtecutli] se le hacía fiesta cada año, al fin del mes que se llama izcalli . . . y ofrecíanle unos pastelejos que llaman quiltamalli, hechos de bledos, y estos mismos comían por su honra.

Libro 1, Cap. 14 (1:32–34). A la honra de este dios [Xochipilli] hacían fiesta, y su fiesta se llamaba xochilhuitl, la cual se contaba entre las fiestas movibles . . . Ofrecían asi mismo dos pasteles que llaman tzoalli . . . y el uno de estos pastelejos era negro y el otro bermejo. La otra gente ofrecía diversas cosas: unos ofrecían maíz tostado, otros maîz tostado revuelto con miel y con harina de semilla de bledos . . . otros ofrecían unas tortas hechas de semillas de bledos.

Libro 1, Cap. 15 (1:36). Cuando hacían fiesta a este dios [Omacatl], que era de noche, comulgaban con su cuerpo; y para esta comunión los principales y teopixques, y los que tenían cargo de los barrios, hacían de massa una figura de un hueso grueso . . . Hecho esto, repartían aquella figura de hueso que habían hecho de masa que se llama tzoalli, y dividíanla entre si, y comían cada uno lo que le cabía.

Libro 1, Cap. 21 (1:48–49). Todos los montes eminentes, especialmente donde se arman nublados para llover, imaginaban que eran dioses . . . El que había hecho voto á alguno ó á algunos montes ó de estos dioses hacía su figura de una masa que se llama tzoalli, y ponialos en figura de personas; no lo hacía él por su manos, porque no le era lícito, sino rogaba á los sátrapas, que eran en esto experimentados y para esto señalados, que le hiciesen estas imágenes á quien había hecho voto.

Libro 2, Cap. 4 (1:89–90). Al cuarto mes llamaban uey tozoztli . . . Todas las muchachas llevaban á cuestas mazorcas de maíz del año pasado, é iban en procesión á la diosa Chicomecôatl, y tornábanlas otra vez á su casa como cosa bendita, y de allí tomaban la semilla para sembrar el año venidero . . . Hacían de masa que llaman tzoalli la imagen de esta diosa, en el patio de su cu, y delante de ella ofrecían todo género de maíz y todo género de frijoles, y todo género de chía, porque decían que ella era la autora y dadora de aquellas cosas que son mantenimientos para vivir la gente.

Libro 2, Cap. 10 (1:97–99). Al décimo mes llamaban xócotl huetzi . . . En lo alto del arbol estaba en pie la imagen de aquel dios [Xiuhtecutli] hecha de masa que llaman tzoalli.

Libro 2, Cap. 13 (1:102). Al décimo tercero mes llamaban tepeilhuitl. En este mes hacían fiesta á honra de los montes eminentes . . . hacían las imágenes en figura humana â cada uno de ellos, de la masa que se llama tzoalli, y ofrecían delante de estas imágenes en respeto de estos mismos montes. Hacían á honra de los montes unas culebras de palo ó de raíces de árboles, y labrâbanles la cabeza como culebra; hacían también unos trozos de palo gruesos como la muñeca, largos, llamábanlos ecatonti; así á estos como â las culebras los investían con aquella masa que llaman tzoal.

Libro 2, Cap. 16 (1:107). Al décimo sexto mes llamaban atemoztli. En este mes hacían fiesta á los dioses de la pluvia . . . Hacían las imágenes de los montes de tzoal.

Libro 2, Cap. 18 (1:109–110). Al mes décimo octavo llamaban izcalli. En este mes hacían fiesta al dios del fuego que llamaban Xiuhtecutli . . . Un tamal hecho de bledos, que ellos llamaban uahquiltamalli, los cuales todo el pueblo ofrecía aquel día y todos comían de ellos por honra de la fiesta.

Libro 2, Cap. 24 (1:134–137). Al quinto mes llamaban tóxcatl . . . Hacían de masa que se llama tzoalli la imagen de Huitzilopochtli, tan alta como un hombre hasta la cinta.

Libro 2, Cap. 29 (1:169–170). Al décimo mes llamaban xócotl huetzi . . . Componían de papeles á una estatua, como de hombre, hecha de masa de semillas be bledos . . . Ponían también tres tamales grandes hechos de semillas de bledos sobre la cabeza de la imagen, hincados en tres palos.

Libro 2, Cap. 32 (1:185). Al décimo tercero mes llamaban tepeilhuitl. En la fiesta que se hacía en este mes cubrían de masa de bledos unos palos, que tenían hechos como culebras, y hacían unas imágenes de montes fundadas sobre unos palos hechos á manera de niños, que llamaban hecatonti; era de masa de bledos la imagen del monte, poníanle delante junto unas masas rollizas y larguillas de masa de bledos á manera de bezos, y estos llamaban yomio. Hacían estas imágenes á honra de los montes altos . . . y hacían unas tortillas pequeñuelas de masa de bledos amarillos.

Libro 2, Cap. 34 (1:192–198). Al décimo quinto mes llamaban panquetzaliztli . . . La estatua de Huitzilopochtli era hecho de masa de bledos.

Libro 2, Cap. 35 (1:200–201). Al mes décimo sexto llamaban atemoztli . . . Componían las imágenes que estaban hechas de masa de bledos, algunos tenían hechas cinco, algunos diez y otros quince: eran las imágenes de los montes.

Libro 2, Cap. 37–38 (1:206–213). Al décimo octavo mes llaman izcalli . . . Las mujeres, toda la gente se ocupaba en hacer unos tamales que llaman huauhquiltamalli, y también en amaneciendo los iban á ofrecer delante de estatua, y así estaba gran cantidad de ellos delante la estatua . . . También ofrecían al fuego cada uno en su casa cinco huauhquiltamalli, puestos en un plato, y también ofrecían sobre las sepulturas de los muertos, adonde estaban enterrados, á cada uno un tamal.

Apendice del Libro 2 (1:215). Tres fiestas se hacían cada año a Huitzilopochtli entre los mexicanos. La una de ellas se hacía en el mes que se llama panquetzaliztli. En esta fiesta á él y á otro que se llamaba Tlacauépan Cuexcótzin, los subían á lo alto del cu, y es que hacían sus imágenes de tzoalli, grandes como una persona . . . Cocían primero la masa y despues formaban de ella las estatuas, en toda una noche.

Libro 3, Cap. 1 (1:262). El día cuando amasaba y hacía el cuerpo de Huitzilopochtli para celebrar la fiesta que se llamaba panquetzaliztli, tomaban semillas de bledos y las limpiaban muy bien, quitando las pajas y apartando otras semillas que se llamaban petzicatl y tezcahuauhtli, y las molían delicadamente, y despues de haberlas molido, estando la harina muy sutil, amasábanla de que se hacía el cuerpo de Huitzilopochtli . . . luego deshacían y desbarataban el cuerpo de Huitzilopochtli, que era de una masa hecha de semilla de bledos, y el corazón de Huitzilopochtli, tomaban para el señor ó rey, y todo el cuerpo y pedazos que eran como huesos del dicho Huitzilopochtli lo repartían en dos partes, entre los naturales de México y Tlatilulco.

Libro 7, Cap. 9 (2:267–268). Antes que llegase ce tochtli, á quien temían mucho por el hambre, todos procuraban de juntar y esconder en sus casas muchos mantenimientos, y todos los géneros de semillas que se pudiesen comer, aunque eran comidas muy bajas, cuales son las que se dicen en este capítulo . . . huauhtli polocayo es la semilla de los cenizos sin limpiar, con todas sus inmundicias.

Libro 7, Cap. 13 (2:273). De la dicha manera hecha la lumbre nueva, luego los vecinos de cada pueblo, en cada casa . . . comían tzouatl, que es comida hecha de bledos con miel, y mandaban a todos ayunar y que nadie bebiese agua hasta medio día.

Libro 9, Cap. 14 (2:380–381). Cuando habían de matar á los esclavos . . . los llevaban al templo de Huitzilopochtli . . . y al tiempo de la media noche . . . apagaban el fuego, y á oscuras daban de comer á los esclavos unas sopas de una masa que se llama tzoalli, mojadas con miel, á cada uno de ellos cuatro bocados.

Libro 10, Cap. 20 (3:127–135). Estos dichos quaquatas, como en su tierra de ellos, es en el valle que llaman Matlatzinco, hace grandísimo frío . . . solamente se da maíz y frijoles, y unas semillas que son de mantenimiento que se llaman huauhtli . . . En su tierra [Michoacán] se dan muy bien los bastimentos, maíz, frijoles, pepitas, y fruta y las semillas de mantenimientos llamadas huauhtli.

Libro 11, Cap. 7 (3:233–234). Una de las hierbas que se comen cocidas se llama huauhquilitl, que son bledos; es muy verde, tiene las ramas delgadillas y altillas, tiene las hojas anchuelas. Los tallos de esta hierba se llaman huauhtli, la semilla se llama de la misma manera; esta hierba se cuece para comer, sabe á cenizos, exprímese del agua en que se cuece para comerse; hácense tamales de esta hierba, los cuales se llaman quiltamalli; hácense tortillas. Es hierba muy comun y comenla mucho; es como cenizos de España. Otra hierba se come cocida llámase quiltonilli; tiene las hojas anchuelas cuando es pequeña. Este hierba es comestible, y cuando ya es grande llamase petzícatl; cuécese con salitre; exprímese del agua para comerla. Esta hierba cría una semilla negra que se llama pítzitl.

D. *HERNÁNDEZ, CA. 1575c.*—

Liber 6, Cap. 44 (2:129–131). Paratur quoque Michuauhatolli, id est Atolli sementiferum ex Michihoauhtli torrefacto hoc semine, et redacto in laevorem cumque exposcit occasio, in aquam conjecto, ea mensura, quae nullam adferat spissitudinem, et densitatem, et insperso melle Metl cocto . . . Est et Hoauhatolli, quod ex Blitis rubeis fit, ingeriturque insperso melle; praeterea Michihoauhatolli, quod ex Michihoauhtli paratur, pisturato nempe Blitorum genere, quod symphoniam a varietate coloris quidam vocant.

Liber 9, Cap. 64 (2:340–341). Reperias in hac Nova Hispania plura Atriplicis agrestis genera, quae universim Hoauhtli, seu Hoauhquilitl vocare Mexicenses consueverunt, et in hortis suis, atque viridariis magna cura serere, atque excolore, qualia sunt Tlapalhoaquilitl, seu Tlapalhoauhtli, radice crassa, brevi, et fibrata, unde prodeunt caules rubei, et in eis folia ejusdem coloris, oblonga, et serrata per intervalla, quae elixa eduntur, suntque adeo grati saporis . . . Praeterea Nexhoauhtli viridis tota, edulisque, et Chichichoauhtli, quae ob amaritudinem locum non habet inter olera, foliis e viridi purpurascentibus, et coccineis floribus, et alia permulta, quorum nec usus est, nec rationem ullam habendam duxi, pro olere magna ex parte eduntur elixa . . . Parant Mexicani e duorum primorum generum semine globulos, ac potionum Michihoauatolli vocatam, qua utuntur velut gratissimo cibo.

E. DURÁN, CA. 1580.—

Cap. 80 (2:85–90). Un ydollo de Huitzilopochtly . . . de una massa que llaman tzvally la qual se hace de semilla de bledos y maiz amassado con miel . . . Las moças del recoximiento de este tenplo dos dias antes de la fiesta de este ydolo de que bamos tratando molian mucha cantidad de la semilla de bledos quellos llaman huauhtly juntamente con maiz tostado despues de molido amasavanlo con miel negra de los magueies despues de amassado hacian un ydolo de aquella massa tal y tan grande como era el de palo . . . tzoalli con miel era la massa de aquel ydolo.

Cap. 90 (2:166). Fiesta de Xocotlhuetzi dios particular de los tecpaneca que son los de Coyoacan . . . el día de su fiesta hacian vn pajaro de massa de simiente de bledos que hemos llamado tzoally la qual massa perpetuamente siruio a estos para efigie de ydolos y carne y guessos de los diosses suyos para despues comerse aquella massa.

Cap. 96 (2:204). La fiesta . . . se llamaba Tepeylhuitl que quiere decir fiesta de cerros . . . Toda la multitud de la gente que en la tierra habia se ocupaba en moler semilla de bledos y maiz y de aquella masa hacer un cerro que representaba el volcan al cual ponian sus ojos y su boca y le ponian en un preminente lugar de la casa y alrededor de él ponian otros muchos cerrillos de la misma masa de tzoalli . . . Sacrificaban esta masa que habian representado los cerros donde despues de hecha la ceremonia se la comian con mucha reverencia. Este día los sacerdotes buscaban en el monte las mas tuertas y corcobadas ramas que hallaban y llevabanlas al templo y cubrianlas con esta masa.

F. GROUP OF RELACIONES, CA. 1580.—

Castañeda, 1580 (218–236). Aculma: Coxen mayz e frisoles e chian e guautli, de que se sustentan. San Juan Teutihuacán: Cogese mucho mais en el dicho pueblo y sus terminos, y frisoles, y guautle y chia para su sustento . . . Tequizistlán: Las semyllas que se sienbran son mayz, chian y huautly . . . Tepexpa: Los mantenimyentos de que sienpre an vsado y vsan son los comunes entre ellos: mayz y frisoles y calabazas y huautli . . . cojen los naturales para sus sustento mayz y frisoles y clabazas y axin y chian y guauhtli.

Castañeda, 1581 (227). Guauhtla: Tienen semillas de mayz, frisoles, calabaças, huauhtli . . .

Contreras Figueroa, 1580 (16–37). Axacupan: Thenyan para su sustento lo que agora tienen, que es pan de mahiz y semylla de bledos . . . los granos y semyllas desta tierra que le sirve de sustento son mahiz, frisoles, agi, chian, guautle, que es semylla de bledos . . . Yetecomac: Las semillas que entre ellos se tienen y se vsan son mahiz, frisoles, chian, guautle, que es semilla de bledos, y de esta semylla se haze vn pan a su modo . . . Tornacustla: Comyan pan de mahiz, frisoles, chian, guautle . . . Tecpatepec: Tienen mahiz, frisol, chian, huautle . . .

Godínez Maldonado, 1581 (287). Tetela del Volcán y Gueyapa: Lo que alli se a cojido y coje es maiz en abundançia, frisol, chia, vautli . . .

González, 1581 (130). Xonotla: Los granos y semyllas que tienen son chian y guahtli . . .

Moniaraz Zamorano, 1581 (310). Quauhquilpan: Se siembra y coge mahiz, avnque poco por la esterilidad de la tierra, y frisoles, y la semilla del huauhtli, que es como grano de mostaza de que se mantienen los yndios.

Pinto, 1579 (p. 92). Iscateupa: Las semyllas de que se aprobechan son frisoles, chian, chile, maiz, pepitas, quilites: destos se aprovechan agora y dicen que siempre antiguamente tubieron estas semyllas.

Pomar, 1582 (p. 49–58). Tezcoco: Los mantenimientos de que antes usaban es de lo propio que al presente usan y se mantienen, que es lo principal el maíz . . . y de huauhtli, y de michihuauhtli . . . el huauhtli, que es una semilla como de nabos, y de su propia color, salvo que es chatilla como lantejas, de que después de molido y amasado hacven unos bollos metidos en hojas de maíz, que cuecen en ollas, ó haciéndola tortillas cocidas en un comal . . . tienen michhuauhtli, que es otra semilla blanca y más menuda: de este hacen bollos por la propia orden que se ha dicho del huauhtli, y de esta suelen beber después de tostada y molida y deshecha en agua miel.

Vera, 1581 (68). Chila: Se da maiz, chile, frisoles, pepitas, chia y guautli.

G. TEZOZOMOC, CA. 1598.—

Cap. 1 (8). Y al tiempo que llegaron á esta ciudad [Tenochtitlán] habían andado y caminado muchas tierras, montes, lagunas, y ríos . . . La comida que traían era maíz, frijol, calabaza, chile, jitomate y miltomate, que iban sembrando y cogiendo en los tiempos y partes que descansaban y hacían asiento, como dicho es, y como liviano que era el chian y huauhtli lo traían cargado los muchachos.

Cap. 3 (15). Allí en Xaltocan hicieron camellones dentro del lago Chinamitl, sembraron maíz, huautli, frijol, calabaza, chilchotl, jitomate.

Cap. 15 (56). Subidos los tecpanecas en un alto de un monte que llaman Axochco, desde allí comienzan á vocear los tecpanecas, diciendo: señores míos, mexicanos, no haya mas, habed clemencia y piedad de nosotros, sosieguen vuestras armas, y reposen vuestras personas . . . os daremos frijol, pepita, huauhtli, chian para vuestro sustento, y maíz por todos los tiempos de los años.

Cap. 48 (209). Llevároníe luego á Toluca á descansar, y en este ínter sobrevino Chimalteuctli, señor de los matlazincas, y díjoles: Señores mexicanos, cese ya vuestro orgullo y braveza, que ya os somos vuestros vasallos y tributarios: mirad, señores, que en esta tierra y pueblo no hay otra cosa sino maíz, frijol, huauhtli, chian, y tea para alumbrar de noche, que es candela, y esteras, petlatl. Esto es, señor, lo que en este pueblo vuestro se dá y cría, y no otra cosa.

Cap. 74 (353). Llegados á Teloloapan partieron la gente en tres partes igualmente, y de las casas que había hechas y habían sido de los muertos, las mejores tomaron los mexicanos; y asimismo los pueblos cercanos á ellos mandaron llevasen maíz, frijol, huauhtli . . .

H. RUÍZ DE ALARCON, 1629.—

Cap. 3 (137–138). Donde mas manifiestamente ay formal ydolotria, es al fin de las aguas, con las primicias de una semilla menuda mas que mostaça, que llaman huauhtli, porque tambien el demonio quiere que le ofrescan primicias: es pues esta semilla mas temprana, endurece y sasonarse qu otra ninguna, y assi la cojen quando el mayz que llaman temprano o nemesina empieça a espigar, que en tierras calientes suscede en dos messes: desta semilla hazen vna beuida como poleadas para beuerla fria, y hazen tambien vnos bollos, que en la lengua llaman tzoalli, y estos comen cossidos al modo de sus tortillas. La ydolatria esta en que accion de gracias de que se aya saçonado, de lo primero que coxen bien molido y amasado, hazen vnos ydolos de figura humana de tamaño de vna quarta de vara poco mas o menos . . . repartiendo los idolillos a pedaços como por reliquias se los comen entre todos.

I. COBO, 1653.—

Libro 4, Cap. 2 (1:337). Hállanse así mismo las yerbas siguientes: Bledos blancos y rojos, y son comida muy ordinaria de los indios, y en la ciudad de Guamanga se hacen de la semilla de los Bledos blancos muy regalados turrones con azúcar.

Libro 4, Cap. 5 (1:350). La Quínua es una planta muy parecida á los bledos.

J. SERNA, 1656.—

Cap. 2 (288–289). Hállase por confessiones de algunos delinquentes, que auía en algunos Pueblos de el Valle algunos viejos, que tenían por officio el sacar el fuego nuevo, que era, segun estoy informado, que este tal Ministro del Demonio, ó sacaba el fuego con vnos palillos, ó lo traian de la vezindad con los poquietes, y alli le offrescian vnos tamalillos de Zoales, que es vna semilla de Bledos, los quales offrescian al fuego, echandolos por las quatro partes de la casa . . . por declaración de vn indio de Cumpahuacan, de donde se tuvo noticia y originó esta complicidad.

K. ANONYMOUS, CA. 1760.—

(31). Otra semilla siembran solos los Jovas, y llaman coguet, ex Mexicani zoale. Es como semilla de quelites, de color amarillo. Su primera cosecha son las ojas de la mata; y la segunda dicha semilla; pero para comerla, la benefician de esta suerte: en una canastita hecha de palma, hechan un almud, ó lo que quieren de dicha semilla, van al Rio, y dentro de el agua lo estan pisando con un pie hasta que rrebienta el grano; y mientras lo pisan, está hechando mucha espuma. Despues lo tuestan, y muelen; y asi rebuelto con agua fria, lo comen; y es un refresco tal de bueno.

L. ANONYMOUS, 1777.—

Fascicles 261–274. Por Agosto tambien, pero solo en barrancas templadas, siembran una simiente, que en la Nueva España nombran alegría, y los tarahumares nombran oguigui. Es á manera de ajonjolí aunque mas menuda y redonda, tostada revienta y crece mucho, y es de mui buen gusto, se cosecha por Noviembre . . . De la alegría tostada, ó comen seca, ó la hacen bebida moliéndola con agua . . . Delas ojas delos bledos (que naturalmente tambien nacen muchos) comen los indios crudas, ó cocidas, y tambien hacen bebida molidas con agua, ô solas, ó revolviéndoles maíz tostado . . . De las semillas delos dichos bledos que son de dos maneras, blanco y encarnado, y al blanco llaman temevalt, y al encarnado chullaca, hacen pan, ó comen tostada, ó hacen bebida.

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